

HOW KENTUCKY BLUEGRASS GROWS*

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INTRODUCTION

Human cultures of widely varying origin have been treading sods of *Poa pratensis* for thousands of years, long before it became known as Kentucky bluegrass. Indifference to the plant's personality has been bred by this long familiarity, with the result that while bluegrass may often be thought of in terms of sod, turf, herbage, forage, or just plain grass, it is only rarely considered in terms of an individual plant. It is the purpose of this paper to describe in simple words what a bluegrass plant looks like and how it grows. In general, only that part of the organization and development will be considered which can be seen with the naked eye or low-power binocular microscope.

The importance of understanding the structure of a plant has become especially apparent in crop plants such as maize where solutions to practical problems—picking, detasseling, cultivating, spraying, cutting, and prevention of lodging—depend for their success on a knowledge of the manner in which the plant is put together. Anderson (1949) has stressed the need for this knowledge in maize and has raised many pertinent questions concerning the maize plant of the future. Bonnett (1935, 1940), in describing the development of the flowering head in barley and maize, has suggested the practical applications of such studies.

In spite of the ever-increasing number of grass farms and suburban homes with ample lawns, little effort has so far been made to relate developmental and morphological studies of forage and turf grasses to practical problems. Knowledge of the individual plant is fundamental to proper analysis of variation in any species, and consequently to the proper appreciation of its genetic possibilities; successful prediction and selection of strains to fit specific environmental conditions depend on such knowledge. Lawn and pasture species are constantly being subjected to management practices of various sorts. An understanding of the basic pattern of development of the plants involved is essential to any attempt to discern the effects of such treatment. Proper statistical planning and analysis of forage production and plot tests must necessarily be based on an appreciation of the variables involved in the normal growth processes of the individual plant. The widely varying and inconsistent results which are frequently obtained in pasture and turf research are probably partly due to the lack of information available on grass mechanics.

*The work reported in this paper was carried on while the author held a special fellowship under a bequest of the late Dr. Malvern B. Clopton. The field work was done at Brookhill Farm, Clarksville, Mo., Dr. Clopton's former estate, and the laboratory work in the Henry Shaw School of Botany of Washington University. It seemed a peculiarly appropriate project, since it concerned the bluegrass pastures at Brookhill which Dr. Clopton knew and loved so well. Grateful acknowledgment is made to Chancellor Compton and to members of the Brookhill Committee for making available this unusual opportunity and to the staff of the Doane Agricultural Service for friendly cooperation in the field. This investigation was submitted to the Board of Graduate Studies in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Washington University.

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METHODS

Problems Involved.—Shortage of data devoted to growth of sod grasses may reflect the subtle difficulties involved in the measurement and description of their growth. Analysis of a wild population of grass is complicated by the fact that plants of different strains and different ages are all mixed up and growing together. Study of these grasses in the laboratory, greenhouse, or even the nursery plot, involves the introduction of artificial conditions which have been shown in several studies (Musgrave, 1940; Ahlgren, et al, 1945) to influence strongly the growth characteristics of the plants. Direct measurement of growing parts can scarcely be accomplished without damaging or removing protecting organs or soil, and consequent introduction of complicating factors. Indirect measurement of growth by examination of a number of plants in a developmental series is based on a number of assumptions which may be difficult to prove. (See van de Sande-Bakhuyzen, 1937).

Preliminary Studies.—Observations on bluegrass growth and morphology were made over a period of two years to provide a general understanding of the problem and the plant. Sods were occasionally dug up, washed, and studied and diagrammed in detail. Special effort was made to discern seasonal trends. From these preliminary investigations sufficient familiarity with the plant was acquired to allow plot tests or laboratory experiments to be made on a small scale. Although the anticipated results were not always obtained, every new condition to which bluegrass was subjected yielded information of some sort. For example, in the course of measuring leaf growth on bluegrass grown in nutrient solutions, it became apparent that all plants of the same origin under the same conditions produced leaves at practically the same rate. Plants could thus be roughly arranged as to time of origin by referring to the number of leaves they bore. Specific periods in the life of a plant could be identified, since each plant that lived through the winter had one leaf shorter than all the rest of the leaves; also certain types of shoots were limited to the cool fall and winter period, while summer buds frequently remained dormant.

It soon became apparent that while the chief concern of the study was to shed light on problems of pasture and lawn, such places were not the best for studying bluegrass behaviour, for an excessive number of complicating factors were involved. Constant cutting maintains the plant in a vegetative condition and seasonal activity is not clearly defined. It was found that the most favorable place to study basic behaviour was in a relatively unproductive old meadow where mowing, treading, and fertilizing were minimum complications and where the grass could be expected to respond only to the strongest seasonal stimuli.

Measurement of Meadow Populations.—A project was then begun on which most of the conclusions in the following work are based. It was decided to measure periodically the last completely exerted leaf on ten plants with respect to blade length, sheath length, and blade width (measured 5 mm. above the ligule). Other data which later came to be recorded in detail included the lengths of the inter-

nodes and panicles on the flowering shoot, the number of leaves which were green, the nodes which bore roots, and the number of tillers and rhizomes. Measurements were begun in early March of 1949 and extended to the following March. During the spring measurements were made weekly, while during the summer, fall, and winter they were made bi-weekly or monthly. Dissection of plants under a binocular microscope was necessary to provide much of this data. To obtain the necessary rhizome material, blocks of sod were subjected to water under moderate pressure until the soil was washed away.

In order to gain preliminary information on variation with habitat, identical studies were made of grass in four situations: the unmowed meadow; a closely grazed pasture; a meter-square plot of meadow grass which had been burned over in mid-February; and a similar-sized plot which had been cleared of all surface vegetation with a sharp hoe while the ground was frozen in February. Although information on all of these plots is not included in the present study, an understanding of the basic trends was facilitated by these measurements and observations.

Supplementary Observations.—Data obtained from the above measurements were supplemented in several ways. Exclosures¹ were placed in pastures being grazed at various times of the year to determine the repercussions of different types of grazing management. Also, a special box was made which had glass sides that could be darkened by inserting a tight-fitting panel. This box was filled with dirt and several plants of bluegrass were placed against the glass. By removing the panel their underground activity could be watched throughout the year.

Information has also been derived from examination of grass plants growing under unique environmental conditions. Plants that grew in soil on which urine or manure had fallen, or that sent rhizomes into mole tunnels, or which had been grazed closely by mice in their winter pathways, or had been covered with alluvium, or grew in deep shade or in very dry or wet localities, have all contributed small bits of important data.

Laboratory Investigations.—In general, laboratory experiments were designed with the idea of finding out how rhizomes grow and what makes them turn up. Some data on leaf growth were also obtained in connection with this work. Bluegrass rhizomes were grown in two ways: separated from the parent plant and grown in water or various solutions in test tubes or Petri dishes; or left attached to the plant and allowed to develop in a natural manner except that they were enclosed in glass tubes so that they could be measured, protected, and identified. Some experiments were made in which these tubes were filled with nitrogen, water, or air.

To obtain as much control over bluegrass plants as possible, some were grown in bottles containing nutrient solution. These were kept under constant light and temperature conditions. In nature, the base of the bluegrass plant, together with its roots and rhizomes, is underground and thus invisible. In searching for some

¹An exclosure is a part of an experimental area which is fenced to eliminate the influence of certain animals, in this case livestock.

manner of exposing these underground parts without too greatly disrupting their natural relationships it was discovered that ordinary "Even-Flow" baby bottles had peculiar possibilities. The nutrient solution could be placed in the bottle and the plant could be held in place above by inserting it through a slightly enlarged hole in the nipple (pl. 2, fig. 1). This would allow the basal part of the plant to be within the nipple and thus protected from desiccation. At the same time, by coating the nipple with opaque paint the inside was kept quite dark, thus simulating soil conditions. The roots could extend into the nutrient solution below and the leaves into the light above.

Rhizome growth was provided for by making five perforations at the base of the nipple, just above the plastic cap, and in these inserting short pieces of $\frac{1}{8}$ -inch glass tubing which were connected at the other end to a $\frac{1}{2}$ -inch glass tube, about 7 inches long, with a 1-hole stopper in the end (pl. 2, fig. 2). As a bud on the basal part of the grass plant was seen to be developing into a rhizome it could be guided into the small glass tube and then would grow out into the larger tube where various experiments and observations could be conveniently made. A perforation was made down through the cap and nipple so that an air-supplying tube could be inserted into the bottle. Saturated air under low pressure was bubbled into the nutrient solution through a fine glass capillary. This air, in escaping, flowed around the roots and base of the plant and out through the rhizome tubes and served to keep the water aerated and the atmosphere in the tubes moist at all times. A light-tight box high enough to accommodate the bottles was then constructed and in the top surface were cut twelve holes spaced on a 9-inch grid (pl. 2, fig. 3). These holes were just large enough to receive the bottle caps. One side of the box was removable so that bottles full of nutrient solution could be inserted into the openings from underneath. The height was made just sufficient so that when the cap was screwed on the bottle, the rhizome tubes inserted into the nipple would rest on the top surface of the box (pl. 2, figs. 2-4).

New rhizomes which had been turned up long enough to form two good leaves and several roots were obtained from a single clone of bluegrass and were inserted into the nipples in such a way that their roots contacted the solution while the bud region of the plant was in the air opposite the openings for rhizomes. In order to keep light away from any rhizomes which might develop, it was necessary to construct a false top of removable panels (pl. 2, figs. 4-5). By loosening a thumb screw these panels could be removed so that access could be had to the rhizome tubes and bottle caps. A fluorescent fixture containing six 15-watt tubes was placed at a height of 30" above the plants (pl. 2, fig. 3).

This battery of bottles was kept first at a constant temperature averaging 70° , and then later at 40° . Variation was not ordinarily more than 5° in either direction. Day length was fourteen hours during most of the experiment but was reduced to twelve hours during the last three weeks of the 40° temperature.

The nutrient solution used was that given in Meyer and Anderson (1941), and was changed every two weeks. A 5 per cent iron solution, made up of equal

quantities of FeCl_3 and tartaric acid, was added weekly. No difficulty was had in getting plants to grow, though the light intensity was apparently insufficient for normal growth, and the leaves were rather lax. The low light intensity at the 70° temperature was not conducive to elongation of buds or roots, while at 40° roots grew well but budding was largely restricted to aerial shoots instead of rhizomes. There was no opportunity for further experiments under more optimum conditions for rhizome production.

LITERATURE

The importance of Kentucky bluegrass as a lawn and pasture grass in northern Europe (especially in Germany and Sweden) and in the northeastern part of the United States has led to many studies on various aspects of the plant. Most of this research has been concerned with seed and forage yields and chemical content under different treatments and seasons. A great deal of intensive genetic work (see Brittingham, 1943) and histological work (see Nielsen, 1946) has been done in connection with its apomictic method of reproduction. Considerable research on bluegrass variation (Smith et al., 1946), taxonomy (Mecenovič, 1939), and germination (Gassner, 1930) has also been published.

Somewhat less information is available on the life history of the plant, its seasonal activities, and its manner of growth. Nishimura (1923), in a comparative study of the morphology and development of *Poa pratensis*, *Phleum pratensis* (timothy), and *Setaria italica* (millet), anticipated by many years subsequent work on the species. Close observation and detailed drawings of the seedlings, the basal region of the plant and of the developing inflorescences were made. Some discussion of germination and roots and the first mention of polyembryony were also included.

Wieland (1926), in connection with an intensive study of variation, necessarily devoted some attention to the gross morphology of the grass, but was not concerned with how it got that way nor how it changed with the season. W. L. Brown (1940), also dealing with variation in the species, traced the seasonal development of two strains from March to October.

Musgrave (1940), in an unpublished thesis on the life history of bluegrass, discussed various aspects of germination, leaf, shoot, rhizome, and inflorescence development, also differences between plants grown as spaced seedlings and in undisturbed sod. Evans (1949) discussed his investigations on bluegrass over a long period of years, including various aspects of its life history and of the influence of environmental factors on its growth. He summarizes information on rhizomes, roots, inflorescences, photoperiodic relationships, and annual cycles of growth, development and reproduction.

Work on the physiological aspects of bluegrass growth has been done by Brown (1939, 1943), Harrison (1934), Peterson (1946), Peterson and Loomis (1949), Phillips (1943), Darrow (1939), Naylor (1939), and others.

Practically no information exists on the developmental anatomy of bluegrass.

The best work of this sort has been done by Sharman on maize (1942) and on *Agropyron repens* (1945 and 1947). He has given close attention to the relationship between the progress of anatomical and morphological events, has emphasized the existence of a common fundamental ground plan in grasses, and has shown how slight changes can produce plants which appear wholly different. McCall (1934) has discussed the developmental anatomy and homologies of various structures in wheat with special reference to the seedling.

Evans and Grover (1940) reviewed much of the literature on the developmental morphology of grass and discussed terminology and general concepts of growth with special reference to the inflorescence in a number of species. Bonnett (1935, '36, '37, '40) and Noguchi (1929) have described and illustrated various aspects of the development of the inflorescences of the small grains and maize. Prat (1934, '35) examined the anatomy and morphology of the grass culm and discussed certain theoretical aspects of its growth. He expressed various correlations, and discussed maturation of tissues.

Certain aspects of the developmental physiology of grass growth have been discussed by such workers as De Ropp (1946), Weintraub and Price (1947), and van de Sande-Bakhuyzen (1937). Important life histories of grass plants include those of Percival (1921) on wheat, Weatherwax (1923) on maize, and Evans (1927) on timothy.

BLUEGRASS IN SIMPLEST TERMS

The Sod.—When we look down at the leaves of grass they merge into a confusion of green (pl. 3, fig. 6). What does an individual bluegrass plant really look like? If we take up a 6-inch square piece of sod the question remains unanswered, for, even after the dirt has been washed away, there is left a confusion of roots and strong wiry underground stems that criss-cross in every direction (pl. 3, fig. 7). These stems seem to connect the various aerial leafy shoots in a haphazard manner. Occasionally they are seen to branch, and some may be white at the tip, showing that they are still pursuing their subterranean destinations. These wiry interwoven stems are called rhizomes, and they are one of the reasons why sod can be rolled up in a ball. They are also one of the reasons why studying an individual bluegrass plant is difficult.

A Single Plant.—If we start with a seedling the problem is simple, but eventually we shall have to deal with the vegetatively spread individual. For our purpose only the gross features of the seedling are significant. Pull a six-weeks-old plant from the soil. It is about as simple as bluegrass ever gets (text-fig. 1A). It has a beginning and an end; it has shed its nourishing grain and become autonomous. It will have four or five narrow spreading *leaves* which are bundled together toward the base for about one-half of their length. At the bottom of the *bundle* are *roots*. If we are used to plants which have stems we shall be disappointed when we pull the leaves apart, for they enclose only the bases of other leaves. At the center of the bundle, at its base, with its tip barely visible, is a

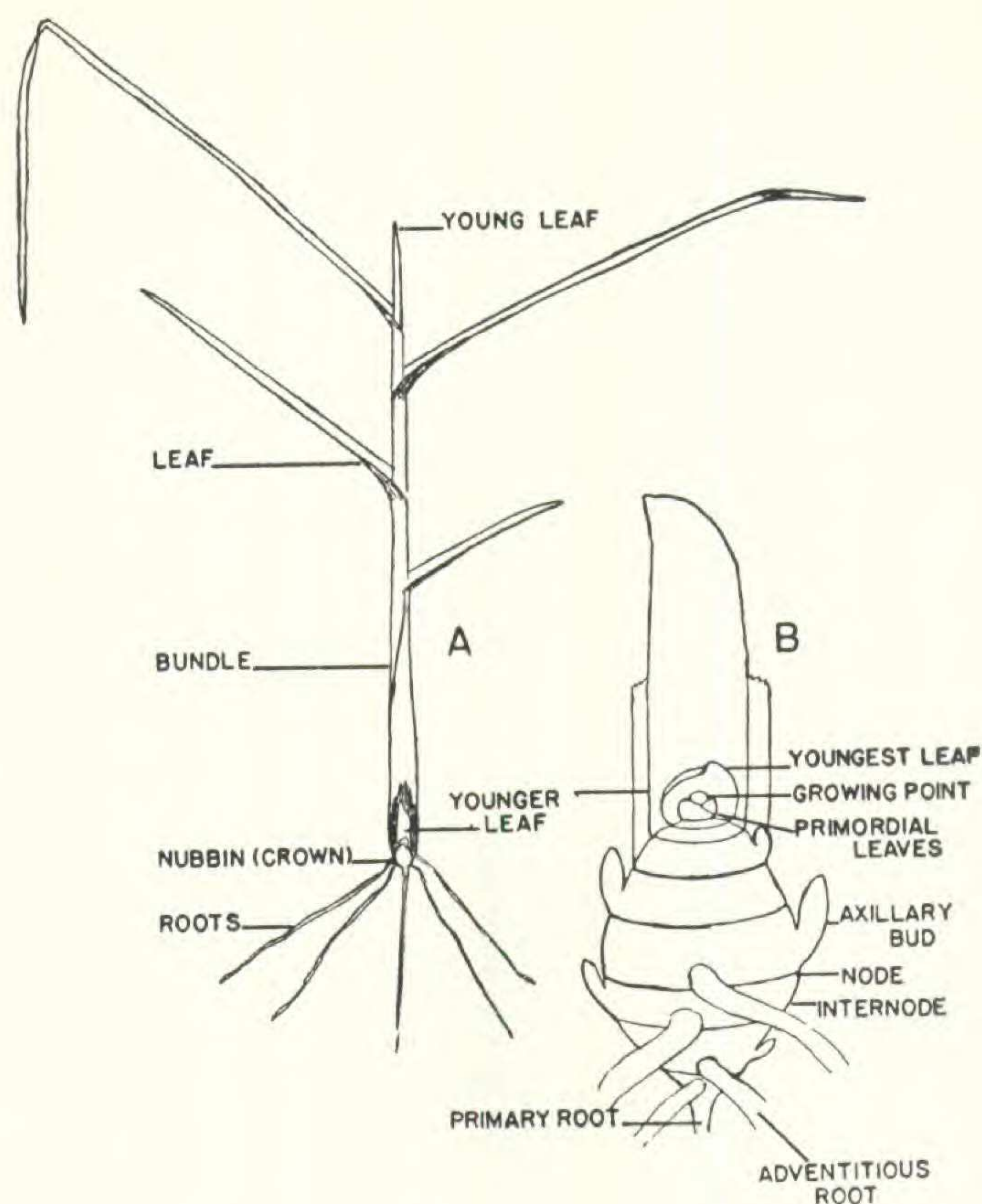


Fig. 1. A six-weeks-old bluegrass plant—about as simple as bluegrass ever gets: A, seedling, $\times 2$; B, crown, $\times 13$.

young, rather yellowish green leaf which is in the process of growing out into the light. Its tip is darker green but it is not yet bent outward as are the other leaves. Within this elongating leaf is a *younger* one only a few millimeters in length and inside of it is the minute *youngest* leaf which protects the nested primordia of two or three future leaves. At the center of this nest is the small bulbous *growing point* of undifferentiated cells, from which the primordia arise. These structures are shown in detail in text-fig. 1B.

The only stem the plant possesses is the *nubbin* of solid material to which the leaves, the growing point, and the roots attach. This nubbin, or *crown*, as it will be called, may be only a millimeter or two in length. Under magnification it is found to be a systematically organized structure with bilateral symmetry, holding alternate leaves and enclosing at the base of all but the lowest one an *axillary bud* (text-fig. 1B). These leaves and buds seem to arise from successive horizontal partitions on the crown which are termed the *nodes*. Separating the nodes are the *internodes*, sections of stem which, while sometimes much elongated, here are scarcely distinguishable.

From each of the lower two or three nodes a pair of roots arises, one root on each side of the axillary bud. These are the *adventitious roots* which play a major role in feeding and anchoring the plant. In all young seedlings there is also a *primary root*, the first root of the newly germinated seed, which persists for a short time at the basal tip. In many species of plants this primary seedling root develops

into a taproot by which such plants are permanently fixed to one spot. But bluegrass is not tied down for a lifetime of sitting on top of a taproot; instead, its liberated stem can develop roots wherever an axillary bud exists, and can thus gradually shift position and still maintain itself.

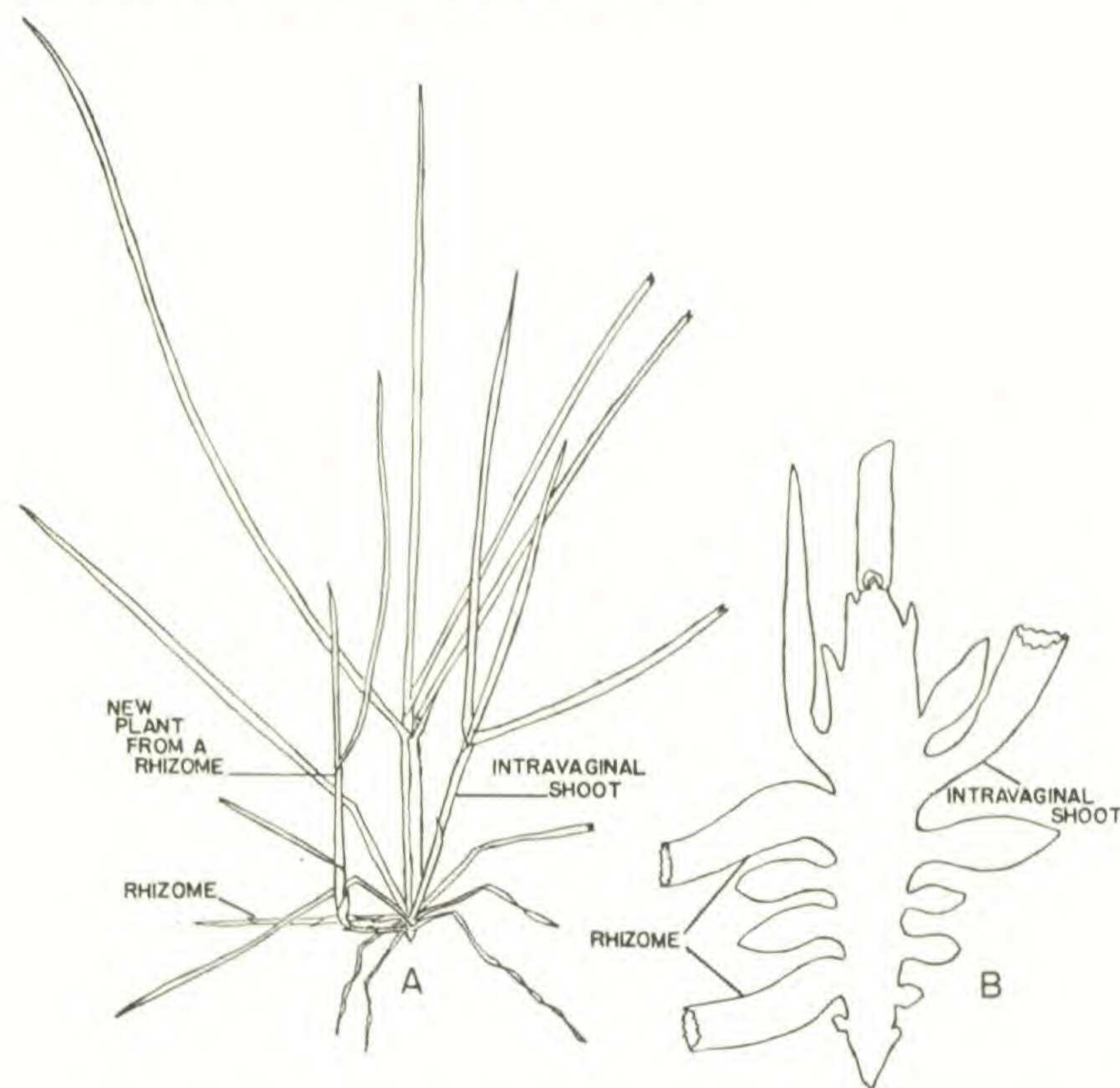


Fig. 2. A spring seedling in its first fall: A, the plant, $\times \frac{1}{3}$; B, crown, \times about 5.

The Appearance of Branches.—When we examine the spring seedling late in the fall of the same year (text-fig. 2A and B), we find that the story has begun to be a little more complicated. The apical growing point is no longer the only active one. Some of the axillary buds, of which there may be 10 or 12 by now, have begun to grow. Thus bluegrass, like most plants, produces branches. A bud has a choice of two destinies. Which it follows depends upon where it is situated. In the fall those buds which are enclosed at the base of the most recent two or three green leaves will send up vertical leafy shoots within the secrecy of the retaining leaves of the parent plant. A few of the lower, older buds borne in the axils of leaves which are dead will develop, or may already have developed, into non-leafy horizontal shoots. The upward-growing branches, or *tillers*, are sometimes called "*intravaginal*" shoots because they arise within the confines of the sheathing base of living leaves. The horizontal shoots are "*extravaginal*" and protrude through the base of the dead sheathing leaf if it is still attached. These are the *rhizomes* which, as we have seen, grow underground. Sooner or later they turn up to form new plants quite similar to the parent.

The differences between tillers and rhizomes are easily seen. One rises in the axil of a green, living leaf, one in the axil of a dead or dying leaf. The most

distinguishing feature of the rhizome is that it has short colorless scale-like leaves and has a distinct stem made up of a series of fairly long internodes, while the upright intravaginal shoot, or tiller, bears normal green leaves and has a very much condensed stem or crown, just as did the parent plant which it resembles in almost every respect.

The end result of this system of branching is that the slender static seedling becomes a mobile plant, capable both of increasing its number of leafy shoots and of extending itself over considerable area, sometimes as much as two square meters in two years time under ideal conditions. (Kannenbergh and Wrede, 1934). The intravaginal shoots thicken the plant by making available more new leaf-producing places, often as many as 10, sometimes up to 50 in a season when there is very active secondary and tertiary branching. Rhizomes spread the plant horizontally, and for all practical purposes once a rhizome has turned up and developed a new leafy shoot it can be considered a new individual, even though genetically it is identical with the parent plant. It may remain attached to the parent for a considerable period, though apparently it derives practically no nourishment from it.

An interesting demonstration of this independence was provided by an experiment primarily designed for other purposes (pl. 4, fig. 8). A flower pot was filled to capacity with soil. A bluegrass plant with long, well-developed roots was placed in the pot so that the roots were covered by the soil but the crown area was left above the surface. A shallow tray with a hole in the center was placed on top of the pot, the leaves of the grass plant being arranged so that they stuck up through the hole. The tray was then filled with vermiculite, a micaceous cutting medium with practically no nutrient value. The buds on the crown were thus surrounded by mica. The soil was kept moist by setting the pot in a shallow dish of water. The mica was watered separately. After the plant became established, rhizomes began to grow out into the vermiculite and turn up along the edges of the tray. It was consistently noticed that after turning up, these new plants grew only very weakly and their leaves were very short, yellowish, and narrow. The parent plant, in the meantime, was deep green, long-leaved, and healthy. Eventually most of the offspring in the tray succumbed. There was no evidence that the vigor of the parent could be conveyed to the second vegetative generation through the rhizome, once it had turned up.

Flowers Develop.—Some time during winter, after intravaginal shoots have been initiated, metabolic changes occasioned by cool weather and short days induce "mature" growing points to begin a process of proliferation which eventually ends up in the appearance of a flowering head. This is a slow sequence of events which begins with a slight elongation of the growing point, the suppression of leaf development, and formation of many small buds which don't elongate (pl. 4, fig. 9). This is the secret winter beginning of the seed-bearing "*panicle*" which becomes so prominent a feature of bluegrass during the month of May. With the advent of longer days and warmer weather multiplication of panicle buds ceases, flower development begins at the end of each bud, and elongation of the panicle

branches takes place. When this is finished, the whole panicle is thrust out of its retaining leaves atop a flowering stalk (pl. 4, fig. 10). This stalk is called a "*culm*" and is part of the main axis which has become greatly elongated. Finally the plant has achieved a conspicuous stem, but only at the price of its own future, since the panicle terminates the growth of the crown's growing point. A plant in its second spring will thus be slightly more complicated than its fall progenitor, because, besides having attached to it various satellite plants in the form of tillers and rhizomes, it will be developing a flowering shoot. The mature individual can thus be said to show three types of shoots: the fall rhizome, the tiller, and a central culm, topped with a panicle (text-fig. 3). All these derive from the basal nubbin of telescoped internodes, the crown. After the inflorescence dies down, the rhizomes and tillers assume the role of perpetuating the plant. Each of these pursues an essentially independent course from then on, and eventually are separated by the decay of the parent.

THE STRUCTURAL UNITS

Leaves.—The leaves of the bluegrass plant have been described as narrow and spreading, but bundled together toward the base. It is useful to distinguish the green spreading parts as the *blades* (or *laminae*) from the lower colorless *sheaths* which in clasping each other form the bundle. The sheaths are slightly compressed tubes, while the blades are flat or folded straps. Successive sheaths enclose each other, but the blades bend outward at their junction with the sheath (pl. 5, fig. 11). A characteristic structure called the *ligule*, a membranous, valve-like flap of tissue, is found at this union and looks like a brief continuation of the sheath beyond the base of the blade (pl. 5, fig. 12).

There are no obvious anatomical differences between sheath and leaf, although, according to Sharman (1942), there is some consolidation of the many small (basipetal) strands of the blade at the ligule and consequently fewer strands in the sheath. In general, however, he minimizes the differences between the two parts. Prat (1935), on the other hand, states that the epidermis of the sheath is more differentiated than that of the blade, and that there is a striking similarity between the epidermis of the sheath and of the internode. In any case, it is apparent that the blade is the primary photosynthetic organ and is always green, while usually the sheath is green only in the vicinity of the veins, if at all.

Just how such a structure as a leaf arises and becomes differentiated into sheath and blade has been well told in detail by Sharman (1945). Although his work was done on *Agropyron repens*, his description of leaf development agrees with that of bluegrass given by Musgrave (1940). Mention has been made of the nest of leaf primordia and the central growing point which lie hidden and protected within enclosing leaves at the apex of the bluegrass crown. The activities of this critical region must necessarily be understood if we are to interpret correctly the growth of the plant as a whole.

The bulbous, translucent growing point (pl. 5, fig. 13) is the source of life,

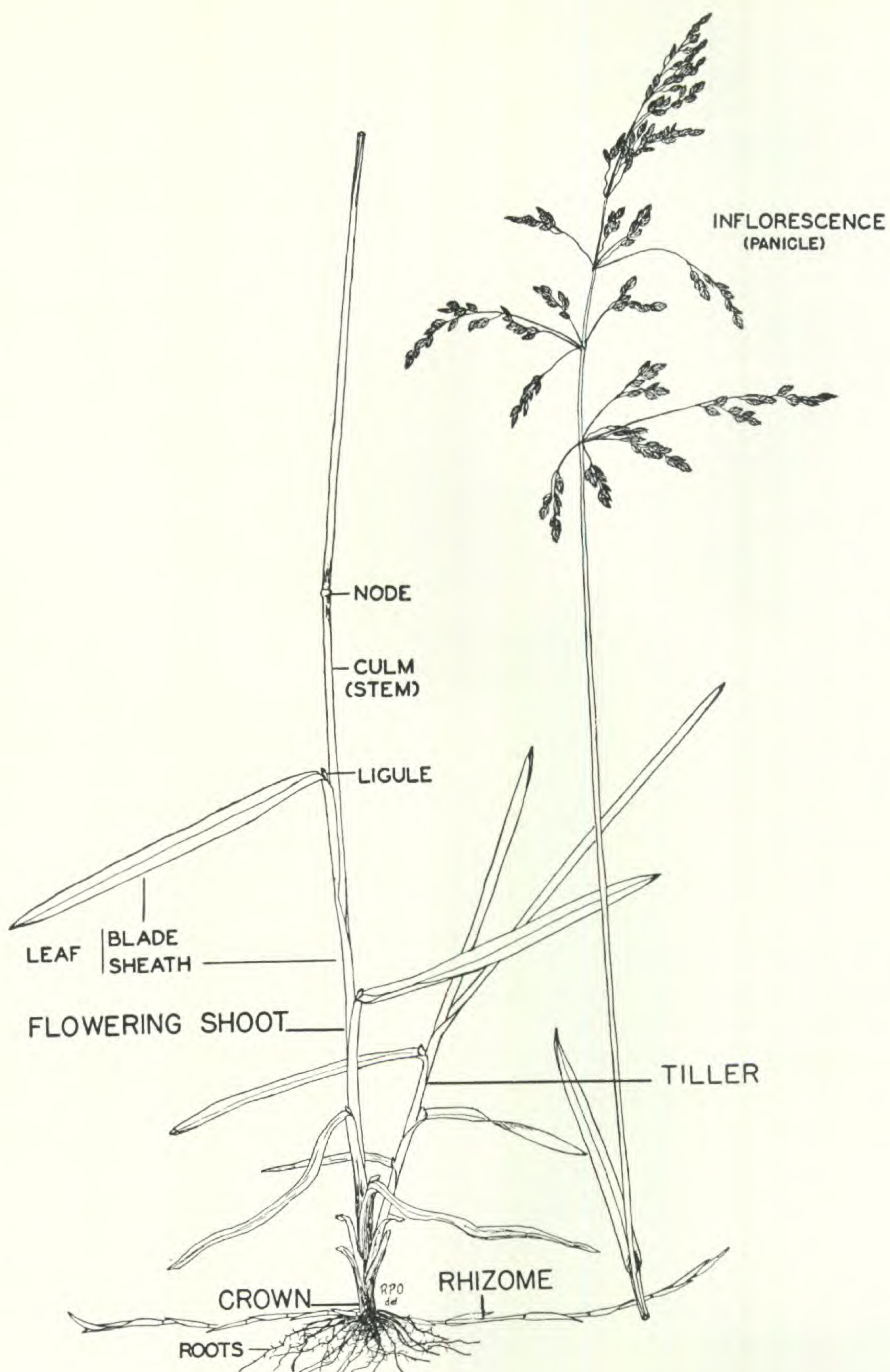


Fig. 3. A mature bluegrass plant showing the three types of shoots which develop from the crown.

the source of new undifferentiated cells from which the plant is fashioned. The first evidence of differentiation occurs when the leaf primordium begins to develop. This starts out as a number of localized cell divisions on one side of the growing point. These divisions produce a small protuberance which soon spreads out laterally, eventually becoming a crescent and finally a complete collar around the growing point. Two of these primordial leaves can be seen in pl. 5, fig. 13. Since the first formed midsection of the collar is able to maintain its advantage over the wings, the collar has an eccentric appearance with the midsection somewhat higher. This incipient leaf grows primarily by cell division at its base and to some extent by a short-lived meristematic band along its tip. As growth continues the collar soon forms a sort of loose-fitting, parka-like hood or cowl over the apex (pl. 5, fig. 14). Through the face opening of this parka the growing point can be seen, and by this time it will have given rise to one or two new crescents. This opening is at first quite minute, .2 mm. or less, just large enough to allow the collar to slip over the growing point. At about this time the leaf is supplied with its primary vascular bundle, and the thin fold of epidermis, the ligule, first makes its appearance at the junction of leaf and crown, thus indicating that sheath tissue is beginning to develop.

Growth of the leaf blade (the part above the ligule) soon becomes very rapid. The face opening of the hood is so stretched out as the blade elongates that it becomes unrecognizable in the mature leaf. Between the time that active elongation begins and the leaf grows to maturity only two or three new leaf primordia develop.² Since the hood stage itself represents about the third primordium in a series it is evident that under ordinary vegetative conditions there are about five or six leaves in various stages of development from the newest collar to the newly matured leaf. These leaves would measure roughly about .1 mm. (crescent), .2 mm. (collar), 1 mm. (hood), 4 mm. (blade beginning to elongate), 50 mm. (sheath beginning to elongate), and 120 mm. (mature). The last two measurements are given only for easy comparison and might be much longer. The first three leaves are waiting in line while the fourth and fifth elongate. The blade and sheath of the sixth have fully matured.

De Ropp (1946), in an analysis of the growth of the first blade and sheath of a rye seedling divided the very young leaf, while it was still in the embryo, into equal sections by marking them with a mixture of lamp black and vaseline. He then made daily measurements of each section for a period of a week. His data showed very well how sheath-growth was delayed until leaf-growth had begun to slow down. It was apparent, however, that the change from leaf-growth to sheath-growth was not an abrupt one, and the growth curve of the entire leaf remained relatively unaffected. This growth was primarily one of cell elongation, since no new cell division was noted after the third day. De Ropp concludes that ultimate leaf length depends on the activity of the basal meristem during the first three

²The interval between the appearance of successive leaf primordia is commonly termed a "plastochrone."

days. This period of cell division undoubtedly varies greatly with species, environment, and season. De Ropp has also called attention to the difference between the manner of elongation of the blade and the sheath. In the sheath it was found that each marked segment contributed about equally to the mature organ. In the blade, however, the basal fourth of the marked primordium contributed three-fourths of the total growth, while the tip segment scarcely enlarged. This may in part demonstrate why the tip of grass leaves is frequently slightly boat-shaped. Apparently, the primordial hood elongates so slightly that its original structure is more or less preserved.

A mature vegetative leaf is thus the product of two growth processes, the elongation of blades and elongation of sheaths. The two processes do not happen to the same leaf at the same time. What actually happens is that an elongating blade (leaf No. 4, for example,) and the sheath of the enclosing older leaf (leaf No. 5) elongate simultaneously and at the same rate so that there is no necessity for the tender young blade point to push up alone through the close confines of the sheath bundle. Instead, the two grow up together. Upon dissection of leafy shoots, the tips of young leaves will generally be found to be just about even with the ligule of the preceding leaf. This is additional testimony to the essentially similar growth rate of blade and sheath. But the sheath does not grow as long as the enclosed blade, and consequently as the sheath matures and its growth stops, the blade within continues its growth alone out into the light. It often happens that the tender new blade is not strong enough to start pushing out of the orifice of the ligule, and the tip of the leaf becomes cramped and crinkled into one or more small folds. These folds remain impressed in the leaf after exertion and are commonly seen on rank-growing bluegrass.

Under vegetative conditions no blade-sheath pair begins to elongate until the previous blade has stopped growing. This has some significant repercussions which will be discussed in detail later.

Phytomers.—Bluegrass is not built of leaves alone. A leaf is only the most obvious part of a more fundamental structural unit called a *phytomer*,³ or plant segment. This unit consists of a piece of stem with a leaf on the upper end and a potential bud or shoot at the lower end. If the leaf is on the left side of the stem at the top, then the bud will be on the right side at the base. There are complementary sections with the leaf on the right and the bud on the left. The two types of sections alternate with each other and produce the characteristic bilateral symmetry of the grass plant (text-fig. 4A and B). Another result of this alternation is that the bud of the segment above rests within the concavity of the leaf below, just above the point where the leaf is attached. This concavity is called the *axil* of the leaf and the bud is therefore commonly called an axillary bud. Though this name is a convenient one, it encourages the idea that a leaf

³*Phy' to mer*, a term according to Evans and Grover (1940) used as early as 1879 by Asa Gray to designate a structure which, when produced in a series, makes a plant of a higher grade. The term was also employed and described by Weatherwax (1923).

and its axillary bud are closely related, when actually from an anatomical and physiological standpoint the association between a bud and the leaf above, on the opposite side, is much closer. Sharman (1942) has provided anatomical evidence supporting this.

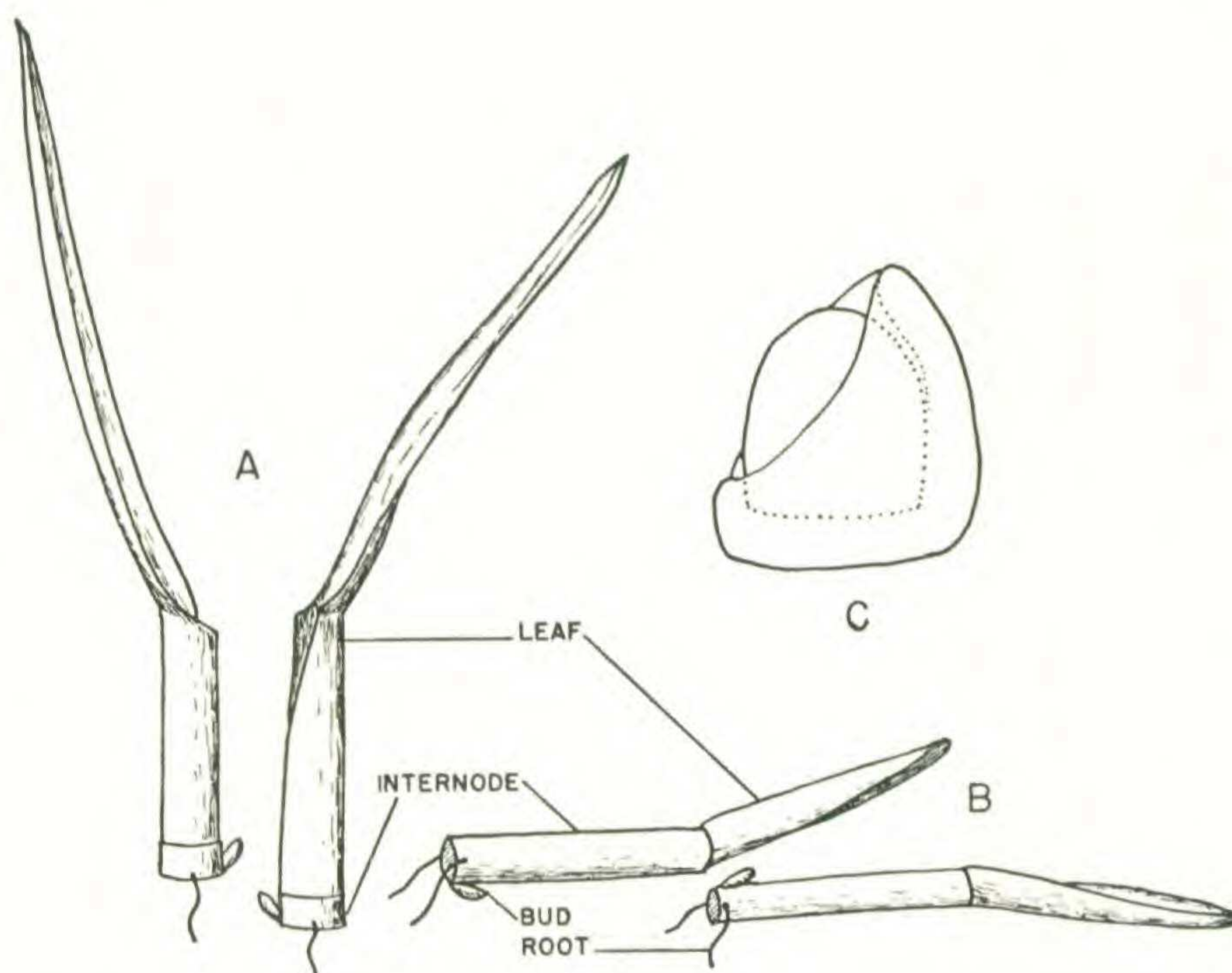


Fig. 4. A and B, complementary phytomers or grass-building units, A, from a vegetative crown, B, from a rhizome; C, the hood leaf which protects the growing point.

Where two phytomers join together a node is formed. The phytomer axis thus becomes an internode which may be long or almost undiscernible. Each phytomer, in addition to its leaf, internode, and bud, is theoretically capable of producing roots at its lower end, usually one on each side of the bud.

Phytomers have their beginning at the growing point. A leaf primordium is the first visible evidence that a new phytomer is forming. The small hood leaf which has been described is not just a shell of tissue tacked on the apex but actually can be visualized as a sort of kettle-shaped structure with a bottom made up of undifferentiated cells produced by the growing point. Inside this kettle new phytomers continue to begin their differentiation as cells in the meristematic point (text-fig. 4C). The course of differentiation and maturation in a phytomer, as Sharman (1942) has shown, is a diagonal one which begins with the development of the leaf at one side at the top, then proceeds to the internode, and passes on to the bud on the opposite side at the base. When roots are present they are the last organs to be formed (text-fig. 5). This course of phytomer development has its basis in the maturation of various anatomical units, especially the vascular system. By the time one phytomer has matured, several others will have begun their dif-

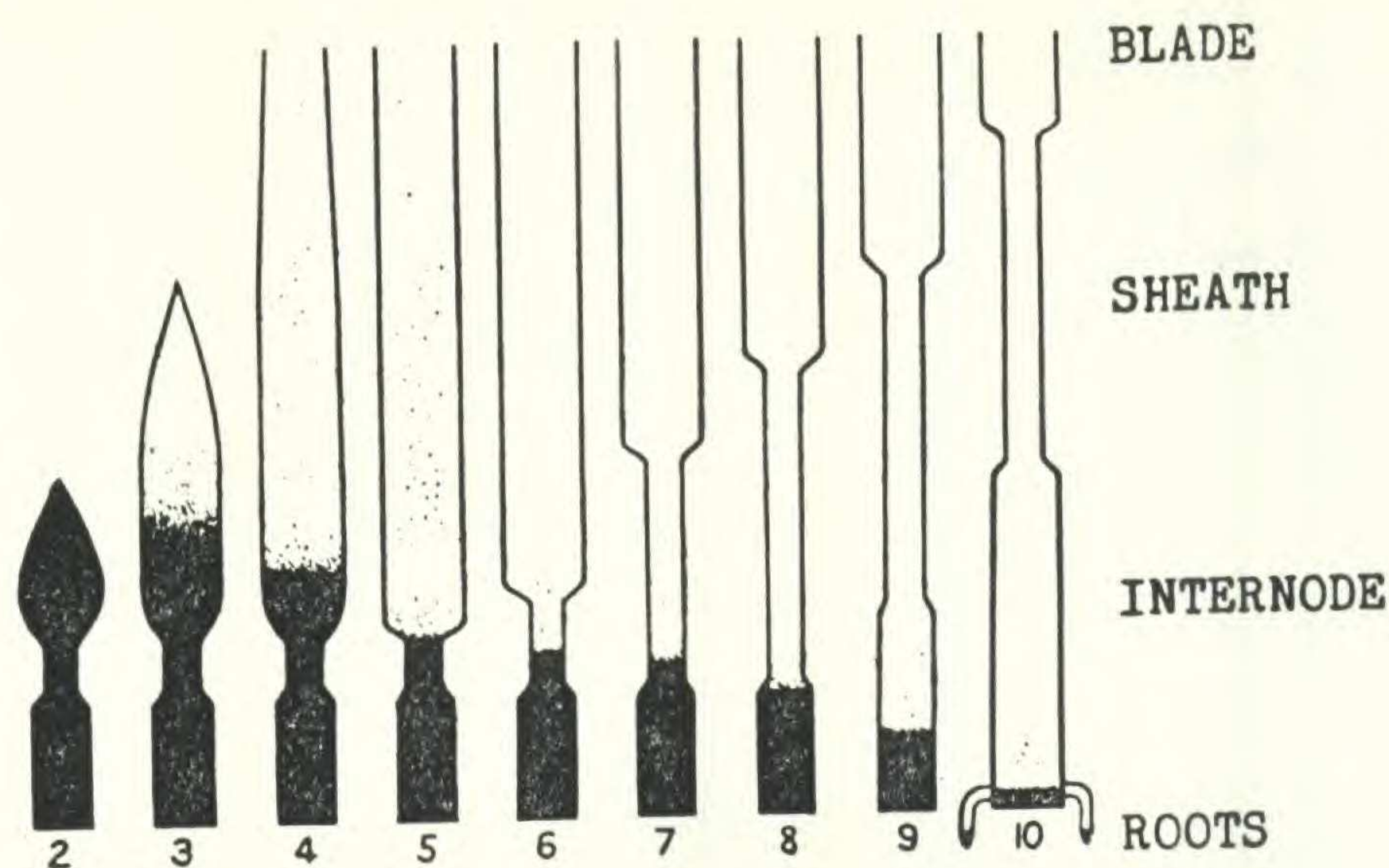


Fig. 5. Diagram illustrating the wave of elongation and maturation passing down the blade, sheath, and associated internode in *Zea Mays*. Solid black indicates the more actively dividing tissues. (From Sharman, 1942).

ferentiation. The exact number depends on the stage of maturity of the plant. Plants ready for flower initiation may have as many as eight or nine segments in various stages of elaboration, while, as we have seen, a vegetative plant may have only five or six readily discernible.

The diagonal course of development is outwardly apparent when we measure the elongation of the different phytomer elements, as van de Sande-Bakhuyzen (1937) has done for wheat. It has been said that the blade elongates first, and is followed by its sheath. In text-fig. 6 the whole leaf has been measured as a unit; consequently successive leaves overlap (or *would* overlap if the growth curve were extended to its origin). This overlap represents that period of time when a sheath and the new blade which it encloses are growing up together. Where there is no overlap, the leaf has grown out of the sheath and continued its growth alone.

The internode may or may not elongate, depending on where it is located on the plant. If it does elongate, it does so only after the leaf has matured. Under vegetative conditions, as in the rhizome, and in the early reproductive phase as shown in text-fig. 6, only one internode grows at once. Under the influence of the inflorescence, however, there is a tendency for some overlap of elongation in those internodes just below the flower head. In bluegrass the last three internodes elongate more or less simultaneously. An overlap has also been recorded by Sharman for maize (1942) and *Agropyron* (1947), by Prat for rye (1935), and is suggested in the last two nodes of wheat (text-fig. 6).

A grass plant thus develops by virtue of its ability to produce new phytomers and to elaborate the plastic organs situated thereon. The remarkable plasticity and independence of these units make possible the varied appearance of different grasses and the different parts of the same grass. This will become apparent with the following description of the three main shoot types in bluegrass.

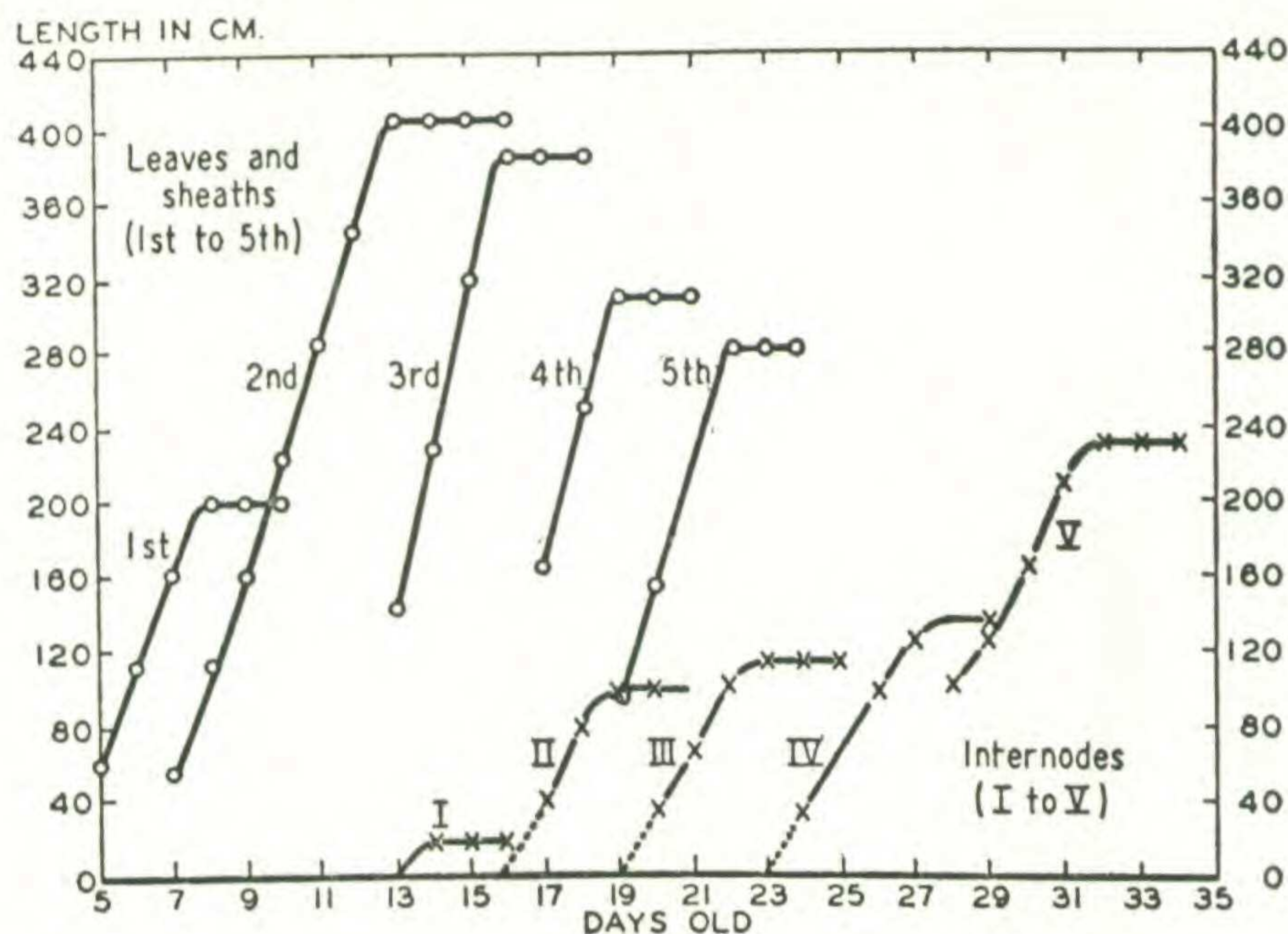


Fig. 6. Growth in length of leaves and internodes of wheat. (From H. L. van de Sande-Bakhuyzen, "Studies on Wheat Grown Under Constant Conditions." Food Res. Inst. Misc. Pub. No. 8, p. 102. Stanford University, Calif., March 1937).

THE RHIZOME

What Does It Look Like?—A rhizome is by definition an underground stem. In bluegrass this means from a few millimeters to several centimeters underground. It may grow horizontally below the surface for 6–12 inches; it may merely swing out and up in a short inverted arch; or occasionally it may turn up abruptly without making any lateral growth, in which case it should probably be considered merely an extra-vaginal shoot. Plate 6, fig. 15, shows rhizomes of these three types on a single plant. The fact that the rhizome is a stem imposes upon it certain responsibilities. It cannot pursue its underground path by simply adding cells at its tip as does a root. Its growing point is obliged to produce phytomers, which in turn produce leaves, internodes, nodes, buds, and roots. The rhizome thus becomes a jointed structure with various appendages rising from the vicinity of its nodes. Internally the separate phytomers are bound together by a complicated vascular system.

The most prominent parts of the rhizome are the elongate white internodes, which, in series, make up the axis. These average 1 or 2 cm. in length, are solid, and are frequently rather flattened in cross-section. The tip of this underground stem is like a sharp white awl and is well suited for penetrating soil (pl. 6, fig. 16). This tip is actually a much-reduced leaf which has no blade. It is essentially a closed tube although a minute pore is present at the tip. It serves well as a sort of caisson within which the subterranean growing point can work to lay down building material and elaborate new structures. When a new rhizome leaf has been fashioned inside, it penetrates the caisson, which then splits and dries up. On

the older parts of the rhizome these leaves hang loosely at each node and become weak brown remnants scarcely recognizable as foliar structures. They are given the special name of *cataphylls*, or scale leaves. These cataphylls are arranged on opposite sides at successive nodes, and partially conceal the internode of the next phytomer (text-fig. 7). In the axil of most cataphylls is an axillary bud, though occasionally no such structure can be found, especially at the first few nodes. A pair of roots usually appears at each node, one root on either side of the bud.

The first two or three internodes nearest to the parent plant are quite short, less than 1 or 2 mm. The next few are intermediate in length, while subsequent ones may range from 1 to 30 mm., apparently depending largely on the amount of water available to the plant. The sequence of cataphyll lengths is essentially similar to that of internodes. At the junction of the main shoot and the rhizome is found the first scale leaf, if such it may be called (text-fig. 8). It has only two prominent veins and arises from the upper side of the rhizome with its back to the crown. It is minute, less than 1 mm. in length, and slightly heart-shaped when it has been broken open. Presumably, it is the undeveloped *prophyll* which will be more completely discussed with reference to intravaginal shoots. The next scale leaf is a short structure, about 2 mm. in length, and is the first true cataphyll. It is well supplied with vascular strands as any legitimate leaf should be. This cataphyll and its axillary bud are not located on the opposite side of the rhizome from the prophyll but are turned only one-fourth of the way around so they are on the side instead of underneath (text-fig. 9). Succeeding cataphylls then alternate first on one side of the rhizome axis and then on the other. If this quarter-twist were not put into effect the axillary buds on the rhizome would point up in the air or straight down in the soil. The first few cataphylls are rather short, but later ones average just slightly longer than their internodes. Cataphylls do not vary nearly so much in length as do the internodes, nor do they appear to be so sensitive to water shortages.

How Does the Rhizome Grow?—The scale leaves are produced from the growing point of the rhizome in the same manner as described for ordinary leaves, except that blades do not develop. When a crown bud has been stimulated to grow into a rhizome, the small enclosing prophyll is broken and successive cataphylls elongate, though only one at a time. Each new scale leaf is a whitish cylinder which tapers to a strongly pointed tip. Since the new cataphyll develops within the previous one (text-fig. 10) there comes a time when penetration must occur. Consequently, the retaining point of the rhizome is broken open at the tip permitting the next cataphyll to appear.

Two main processes occur on every phytomer: one is leaf growth, one is internode growth. On the rhizome, elongation takes place first in the cataphyll, then in the stem behind it, thus following the pattern described for phytomers in general. The scale leaf is extended not only by its own growth but by that of the internode below. It can be seen, therefore, that the penetration of one cataphyll by another is not simply a matter of one leaf growing up inside the other but is the product of two separate forces, leaf elongation and stem elongation.

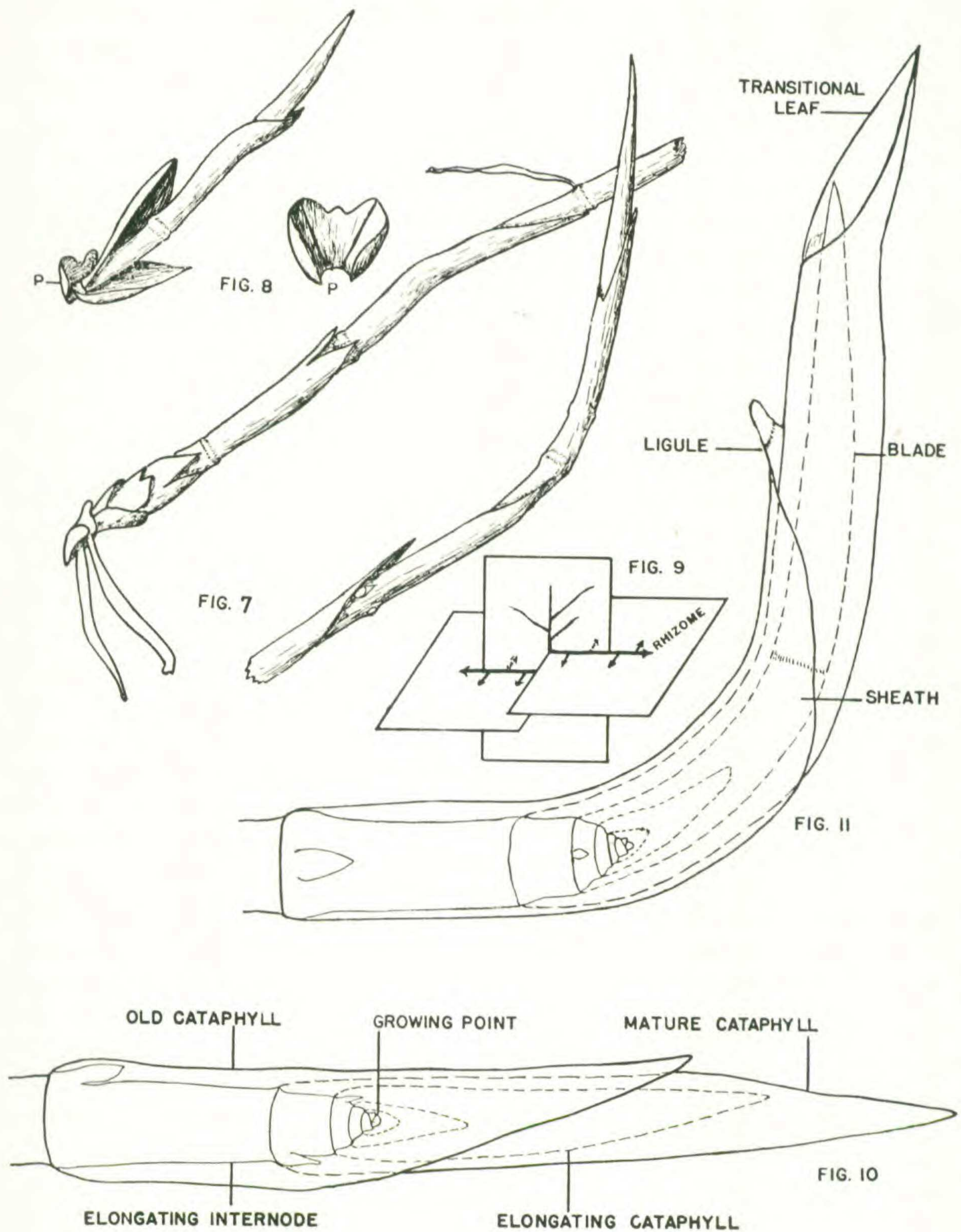


Fig. 7. A rhizome, $\times 4\frac{3}{8}$. Fig. 8. First leaves of the rhizome, $\times 4\frac{3}{8}$ (P, prophyll). Fig. 9. Showing the arrangement of branches and buds on the bluegrass plant. Fig. 10. Diagram of a rhizome tip. Fig. 11. Diagram of a rhizome tip which has begun to produce cataphylls tipped with blades and is turning up.

One might describe the growth of the cataphyll as the forging of a steel tip. Once the tip is forged the developing internode serves as a shaft by which the tip is pushed out of the old cataphyll and through the soil. While this is going on, a new point is again being forged within the confines of the tip in use. Sooner or later the tips of the cataphylls become more delicate, a little less conical and a little more flattened. Upon close examination it will be seen that the point (only 1 or 2 mm. in length) is no longer a complete cone with a small pore, but is slit down one side (pl. 6, fig. 17). Furthermore, if we open this slit carefully we will find the slit point is separated from the rest of the cataphyll by a thin perforated membranous diaphragm which is the ligule. This new, longer, open point thus represents the first beginning of a leaf blade on the cataphyll. It is common to find many cataphyll leaves tipped with very short blades, but wherever this tip, by virtue of the removal of some physiological block, is allowed to reach a length of 4 or 5 mm. it is apt to be associated with a curving up of the rhizome and with its prompt appearance at the soil surface (pl. 6, fig. 18).

How Does It Turn Up?—In many respects we should not speak of a rhizome's turning up at all, for very little, if any, bending originates in the internodes, nodes, or cataphylls of that structure, even though they may become secondarily curved by playing follow-the-leader with the new blade (text-fig. 11). This blade, in contrast to the indifferent sheath, has a strong objection to gravity, and as soon as it has exceeded the limitations of its enclosing cataphyll it shows this prejudice by striving to reach upward to the soil surface. This change from no blade to a fairly long blade (several cm.) is sometimes a sudden one, in which event only one leaf is required to make the break. The fact that the longer blade is usually associated with a longer sheath makes this a possibility. On the other hand, progress toward a long blade is sometimes slow, and two or three leaves may be involved in the effort to reach above ground.

Once a bladed leaf reaches the light, no elongation of the internode beneath ordinarily takes place. Light, working through the blade, prevents internode growth. Weintraub and Price (1947) investigated the physiological basis of such inhibition in the oat seedling and showed which wave lengths of light cause the inhibition, but they did not isolate the photo-receptive substance. If blade-tipped cataphylls do not reach light, the associated internode will elongate. When a leaf with a long well-developed blade is prevented from reaching the light by being covered with soil, manure, or other debris the internode will become abnormally long (text-fig. 34). Where the transition from cataphyll to aerial leaf is abrupt, the rhizome shoot has a characteristic abrupt right-angled appearance, but where the transition is slow and internode growth takes place within the upbending leaf, the rhizome is gracefully curved. The manner of turning up, which varies greatly with habitat and strain, has a distinct influence on the depth and angle at which the crown of the subsequent shoot comes to rest.

Every aerial leaf which develops from the underground growing point follows the course of the transitional leaves, since each new leaf blade arises within the

previous sheath. Successive leaves increase in length, and later development of the crown is similar to that already described for the seedling. In pl. 6, fig. 18, the last roots on the top rhizome indicate the position of the growing point within enclosing sheaths.

The most important result of this turning-up process is that the growing point of the shoot is usually left submerged in the soil to a depth of 1–3 cm. This is of great value to a pasture and lawn plant which must withstand close grazing, treading, and mowing. Of significance also is the accumulation of a well-protected reservoir of subterranean buds in the crown area which can provide new rhizomes on a minute's notice. It will be noted in text-fig. 11 that usually the rhizome axis remains essentially horizontal and its buds point in the same direction as the rhizome. This exerts a directional influence on new rhizomes which develop. It explains in part the maintenance of a general similarity of direction from one generation of underground shoots to the next. As the shoot becomes older the crown becomes more vertical and the buds more crowded; new shoots then develop in almost any direction.

Why Does the Rhizome Turn Up?—The turning-up of a rhizome is usually not due to the influence of the environment on the rhizome itself, although mechanical obstruction sometimes plays a small part. Instead, turning-up seems to be correlated with some physiological development within the parent plant. Sharman (1947) has mentioned the fact that light reaching the rhizome was not the deciding factor in *Agropyron repens*, for rhizomes of that species will continue to grow horizontally (though they turn green) when the soil around them is removed. Similarly, above-ground stolons of many grasses and rhizomes of other plants such as the common *Sansevieria* have reduced leaves and remain prostrate regardless of their being exposed to light.

With bluegrass, rhizomes artificially exposed usually begin to form blades and shorter internodes, and soon turn up. The number of transitional leaves, however, may vary considerably. That the rhizomatous habit in this species apparently hangs in a fairly delicate balance is suggested by various experimental results and observations. Harrison (1934) has found that rhizomes tend to be much shorter when grown in a high nitrogen medium. Brown (1939) has presented data that show decreasing rhizome length above a temperature of 70° F. and below 60° F. Heavy clipping and grazing also reduce rhizome length. In early spring and early fall, when above-ground growth becomes more proteinaceous and darker green and when carbohydrate reserves are drawn on heavily, practically all rhizomes below the ground begin to appear at the surface.

Laboratory Experiments.—In a series of experiments, the growth of rhizomes was studied under controlled conditions. The rhizomes were separated from the parent plant and placed upright in test-tubes containing a little water, or in Petri dishes on blotter paper. These were then grown in the dark, and were subjected to the following treatments with the results indicated:

TABLE I. GROWTH OF RHIZOMES SEPARATED FROM PARENT PLANT

Number of rhizomes	Aver. initial length (cm.)	Grown in	Temp. (°C.)	Days	Treatment	% increase in length
4	3	Tubes	70	14	Tube filled with water	0
4	3	Tubes	70	14	Tube filled with nitrogen	0
4	3	Tubes	70	14	Tube filled with air	50
5	6.4	P. dish	40	14	Distilled water	24
5	6.0	P. dish	40	14	Auxin, 1 mg./liter	20
5	6.1	P. dish	40	14	Auxin, 10 mg./liter	32
5	5.6	P. dish	40	14	Auxin, 50 mg./liter	28
5	5.4	P. dish	40	14	Distilled water	33
5	5.7	P. dish	40	14	Iodoacetate, .00001 m.	19
5	6.4	P. dish	40	14	Iodoacetate, .0001 m.	10
5	6.0	P. dish	40	14	Iodoacetate, .0005 m.	15
5	6.2	P. dish	40	14	Iodoacetate, .001 m.	19
9	5.0	P. dish	40	38	Distilled water	34
18	5.0	P. dish	40	38	Glucose, 1%	88

While in general the numbers of rhizomes used were insufficient to lend significance to the small differences indicated above, the response to glucose is clear, and a slight inhibiting effect of iodoacetate is strongly suggested. All rhizomes which made any growth showed a distinct tendency to turn up. Glucose rhizomes continued alive for 3½ months and eventually increased on an average of 125 per cent in length, while the distilled water controls showed almost no growth after two weeks, and were obviously dead after one month. Figure 19 of pl. 6 shows control and glucose rhizomes removed from the Petri dish for comparison.

Another group of experiments utilized the rhizome while it remained attached to the parent plant. In this group test-tubes were supplied with rubber stoppers in which there were three holes. Into two of these holes right-angled glass vent tubes were inserted. The rhizome of a bluegrass plant was inserted into the test-tube through the third smaller hole and was then sealed in with a little cotton saturated with lanoline paste. The entire plant could thus be conveniently held in place by fixing it between the vent tubes. The test-tubes with their respective plants were then placed in a flat and covered with vermiculite so that no light could reach the rhizomes. The plants were in a perfectly normal position and could produce leaves and roots in their usual manner. The bent glass tubes enabled the rhizome chamber to be filled with air, nitrogen, or water. Three tubes were left with free access to air; three were filled with distilled water and corked up; and three were flushed with gaseous nitrogen for ten minutes each week and were then sealed.

All rhizomes grew well, though all showed development of leaf blades and a concomitant effort to turn up. In some cases later leaf blades became much shorter and practically scale-like after the parents became well established. Growth averages of the rhizomes in each treatment over a period of four weeks were as follows:

Tube filled with	Total growth
Air	7 cm.
Nitrogen	6.5 cm.
Water	6 cm.

Two of the air rhizomes continued to grow for six weeks longer, increasing in length by 23 and 29 cm. There were approximately 15 phytomers on each of these, produced over a total period of ten weeks. This average of one new phytomer every four to five days is somewhat less than that achieved under completely natural conditions. In this experiment the vermiculite medium was sterile and not favorable for perfect development.

These experiments were not designed with any idea of statistical demonstration of facts, but were rather trial runs to perfect techniques. The indications are fairly clear, however, that while *isolated* rhizomes apparently will not grow in water or nitrogen they will grow to some extent in air, and will remain alive longer and grow more when supplied with sterile glucose than with distilled water only. In every case where growth occurred rhizomes began to turn up. No treatment prevented this.

Rhizomes remaining on the parent plant were able to grow equally well in gaseous nitrogen, distilled water, or air, and it happened that those in air outlived those in other media. In these rhizomes there was a strong tendency at first for leaves to develop, and for the tips to turn up. Later leaves, however, were much reduced. It is apparent that the rhizome has distinct possibilities in the field of experimental growth study, especially because of its natural independence of light. With the use of a complete nutrient solution and various hormones and inhibitors information might well be obtained on controlling factors in leaf differentiation and geotropic responses.

Internode Lengths.—The internodes of rhizomes are delicate recording devices. Their lengths are highly variable and apparently indicative of some fairly fundamental condition in the parent plant. A considerable number of rhizomes were dug up occasionally during several summers and each one was plotted on a graph on the basis of its sequence. In a given year a remarkable similarity of pattern was found to prevail in rhizomes from different plants and habitats.

Text-fig. 12 shows diagrams of a few of these underground shoots dug from several localities during July, 1948. Not only is there a similarity of pattern, but also a strong correlation of phytomer numbers. The consistent reduction in internode length to a few mm. in all of these shoots was evidently indicative of a period of drought which occurred during May and early June. In rhizomes dug up in July, 1949, no such depression of length was seen, and the possibility that day length played a part was thus eliminated. The rainfall records given in text-fig. 12 show that there was no shortage of moisture in 1949.

The conclusion that dry soil results in short internodes agrees with the observation that excessively drained sites showed shorter average internode lengths (text-fig. 13). The data of Phillippe (1943) are significant here in that they show *no*

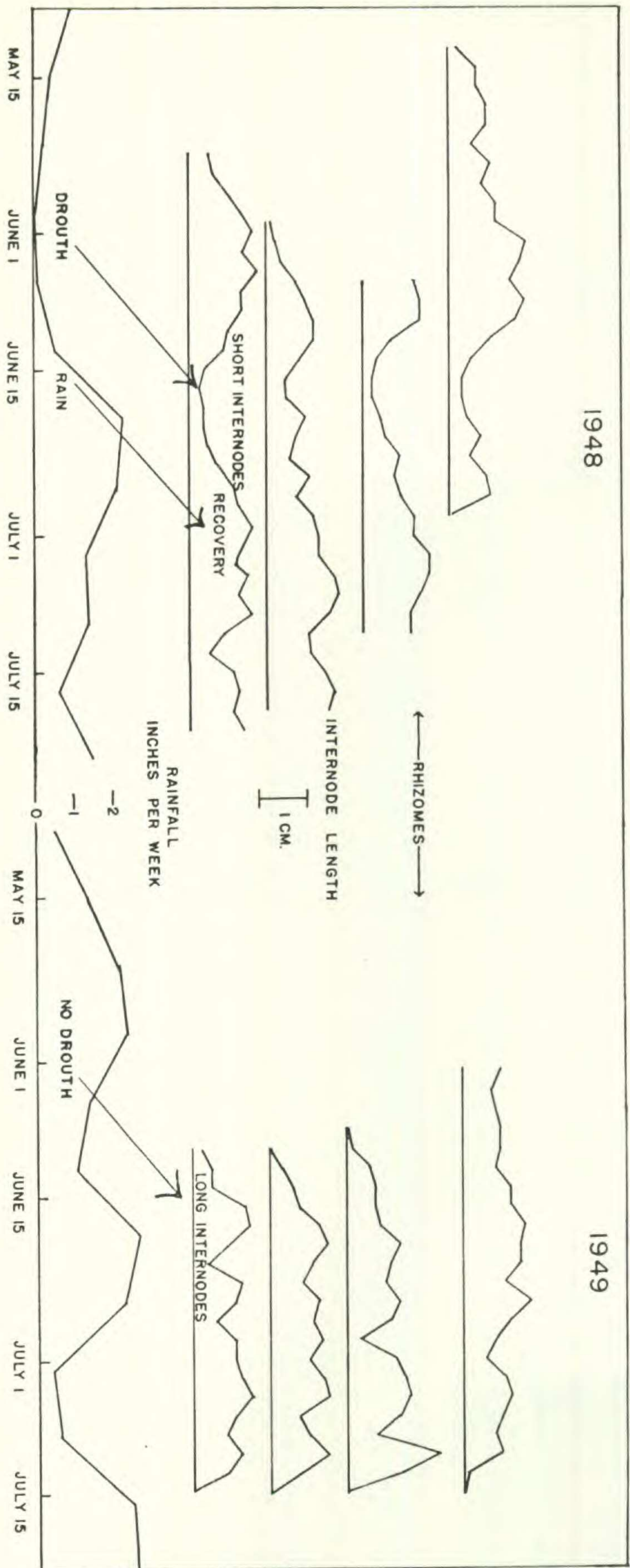


Fig. 12. Rhizome internode lengths of two years compared with rainfall records. Each curve represents a rhizome and shows the length of its successive internodes. Drought in 1948 produced short internodes; 1949 showed no such depression.

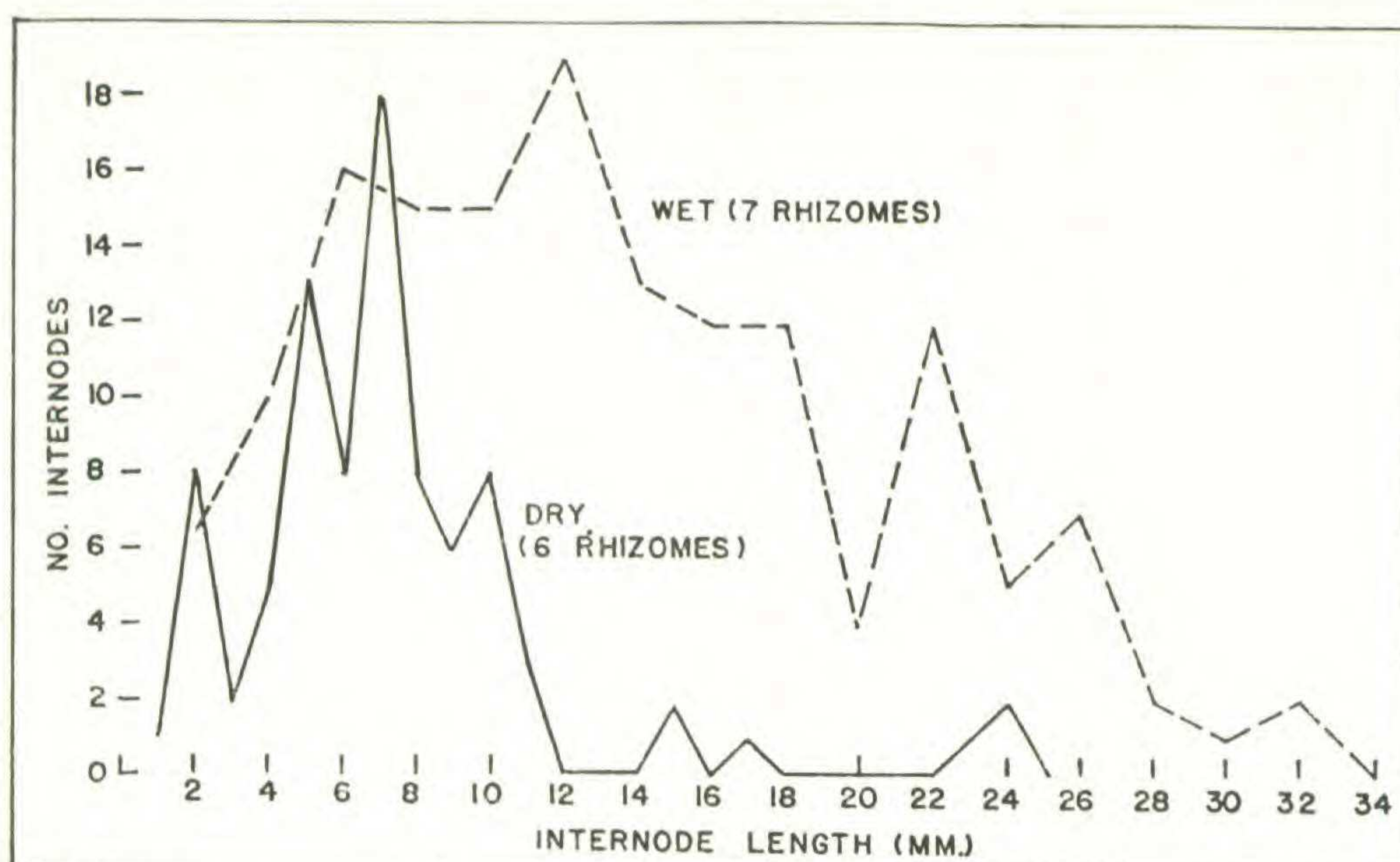


Fig. 13. The number of internodes of given lengths on rhizomes collected from two good soils, one of which was excessively drained.

correlation between internode lengths and various levels of potassium, nitrogen, or phosphorous in his nutrient solution cultures of bluegrass.

By matching and superimposing the patterns of a series of rhizomes dug up at different intervals during a year, a complete sequence of rhizome growth from some time in late May up to fall could be prepared. The sensitivity and uniformity of rhizome growth would seem to offer some interesting possibilities in interpreting the past history of a sod and related environmental and climatic conditions.

When Do Rhizomes Grow?—A seasonal interpretation of rhizome growth is not simple. About the only time that one cannot find a few rhizomes still pursuing their underground path is in late winter and early spring, and there are even some exceptions to this. Wherever rich soil is kept warm and moist during winter by circumstances such as proximity to heat pipes and buildings, or in alluvial soils close to the water table, rhizomes which are especially thick and white can usually be found. Even these, however, ordinarily turn up with the advent of spring.

There is one period when rhizomes are almost always found just beginning to grow, and that is when inflorescence elongation begins. From that time on through the rest of the summer rhizomes appear from subterranean axillary buds and grow at length through the soil. By late August most of these have turned up. At this time there is frequently a very brief flush of new short sprout-like rhizomes which are described in detail in the following section. For a few weeks in late September or early October, when the leafy tops are growing rapidly, there will usually be a second period when few new rhizomes can be found still underground. A great deal depends on just how rapid the fall flush of growth is. In dry years greening may be so slow that cessation of rhizome growth is not very abrupt, and possibly may not occur at all.

Production of rhizomes in *late* fall depends again on seasonal conditions and habitat. It is highly variable, but in general some buds do develop and grow a few inches. These late rhizomes are often caught underground, or just at the surface when the soil freezes. They then wait for spring thaws, as do the underground parts of many early-developing spring plants.

Rhizome Types.—Rhizomes are not all the same. Some turn up almost immediately without ever making a long internode and look much more like intravaginal shoots except that they do not develop inside a living leaf of the parent plant (pl. 6, fig. 15). Under a few conditions rhizomes are inclined to be *stoloniferous*; that is, instead of growing underground they grow along the surface of the soil and usually bear well-developed leaves instead of cataphylls. Those rhizomes which grow underground are also of various types. Some, such as those grown in the box, grow down and then up in a broad curve, while others grow horizontally just below the soil surface. Some are delicate and wiry, others fat, white, and flattened on the side.

Rhizomes differ greatly in their tendency to branch. Generally, in established sods axillary buds are suppressed. If the terminal bud is injured, however, then one or more of these rhizome buds develop. Under especially favorable growing conditions vigorous rhizomes will branch voluntarily (pl. 7, figs. 20 and 21, left). Evans and Ely (1935) found that in spaced plants grown in a nursery plot about 10 per cent of the rhizomes showed some branching, and that as a result of branching some clones or plants of bluegrass gave rise to as many as six vegetative generations a year. Branching also occurs when an actively growing rhizome is exposed to bright sunlight accidentally, before it is prepared to turn up. In this case branching is limited to the last few nodes, and the branches do not have long white internodes but turn green and bend upward immediately. The development of branches apparently depends on some critical balance which can be altered by environmental conditions. As with every other characteristic of the bluegrass plant variation with strain is also evident.

There are also some fairly striking seasonal differences in rhizomes. In general, summer rhizomes pursue a deliberate underground course, extending the plant to some distance. These might well be called *extensor* rhizomes. They result when a developing bud feels some distinct obligation to remain underground and not to produce leaf blades except as a last resort. Figure 21 of pl. 7 shows examples of this type. Other rhizomes might well be termed *sprout* rhizomes, for they seem to be a response to a different combination of conditions in the parent plant. They represent a sort of desperate effort to perpetuate the parent plant in the face of some adverse condition. Such rhizomes are short and are characteristically found on plants which have been injured in some manner. They may arise from a crown or from another rhizome. Plate 6, fig. 19, shows the extreme type of sprout, developed from a separate rhizome very short on food reserves. Harrison (1934) shows similar sprouts from rhizomes of plants which were injured by high temperatures. During a brief interval from late August to early September, just be-

fore rapid fall growth begins, many short sprout rhizomes appear from the crowns of plants which have been burned, grazed, or mowed too close, or, weakened by rank growth, allowed to accumulate on the sod. Such sprout rhizomes play a very essential part in the perpetuation of rank meadow bluegrass, and are especially common on those plants which have bloomed during the previous spring (pl. 7, fig. 22).

While rhizomes may be given names they themselves are not cognizant of any classification and may be intermediate in length, function, and appearance. Thus a pasture which has been grazed throughout the summer seldom contains any long extensor rhizomes. They are usually a sort of half-breed type, and are produced all summer long and well into fall.

THE TILLER

The tiller resembles a seedling or a turned-up rhizome in having green leaves and a nubbin of short root-bearing internodes at the base (pl. 7, fig. 23). This shoot arises, however, directly from an axillary bud (text-fig. 2; pl. 7, fig. 24) and not from a seed or from the tip of a subterranean stem. As pointed out earlier it develops in the axil of a living leaf.

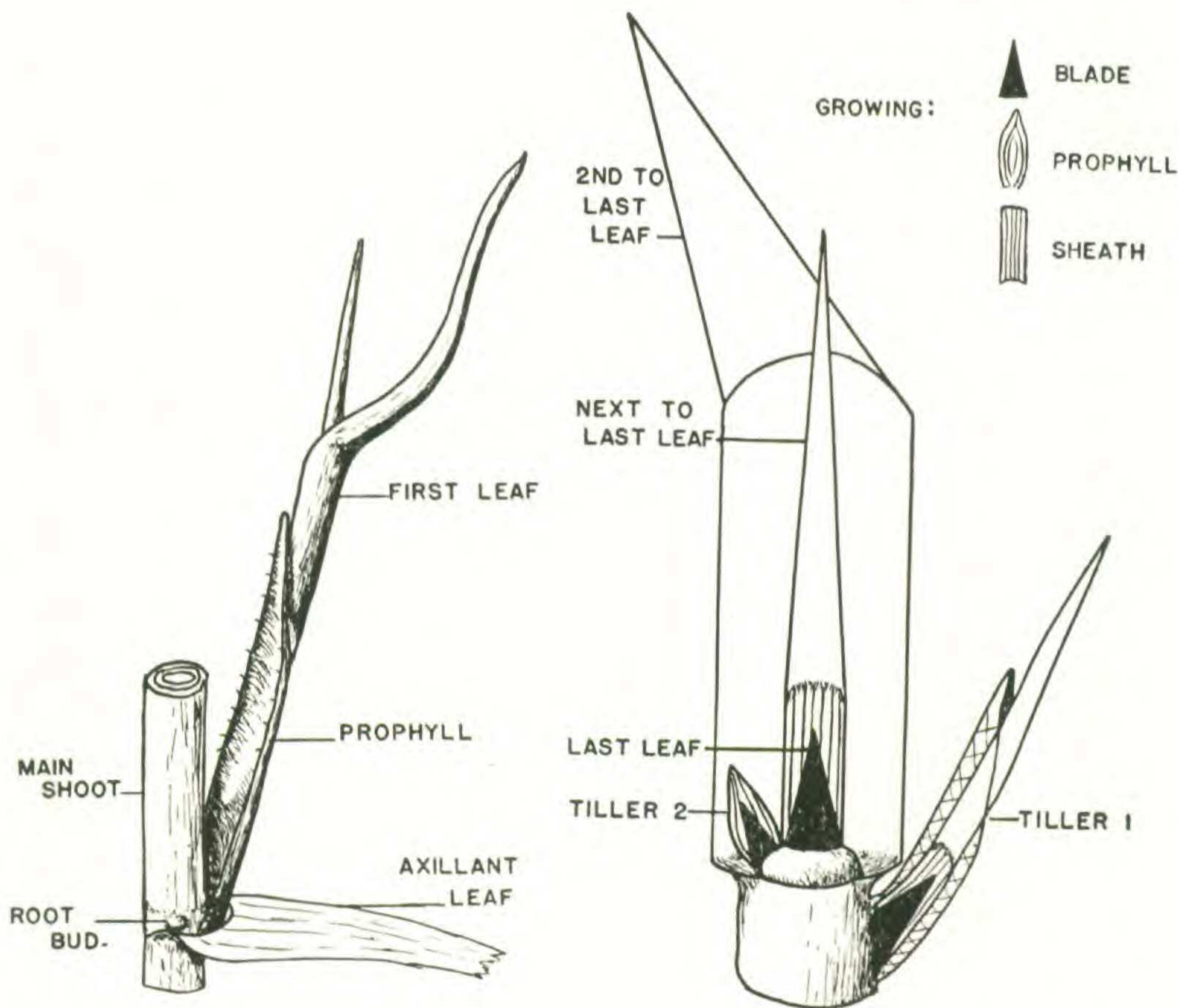


Fig. 14. The first organized structure to develop from an axillary bud is the prophyll. It sheathes the first leaf.

Fig. 15. The parts of the plant which grow at the same time during the fall "shooting season." See Table II.

The Prophyll.—Morphologically the tiller is distinctive only in the possession of a well-developed *prophyll*, or pre-leaf (text-fig. 14; pl. 7, fig. 25). This small insignificant structure is seldom seen or examined closely, for its life is short and its purpose quickly served. It is the first organized structure which develops from an axillary bud (Sharman, 1945). It does not look like an ordinary leaf for it has no blade. It is a semi-membranous sleeve, about 2 to 3 cm. long, which is flat or somewhat grooved down the side nearest the main shoot. In cross-section it is semi-circular or somewhat crescent-shaped, and at each edge of the crescent is a prominent vascular strand which extends from the base of the prophyll to its tip. Very small strands may be visible along the outer rounded edge. The prophyll is a completely closed tube except for a small pore at its tip which represents the opening left when the primordial prophyll slipped over the growing point. In this and many other respects it is similar to the cataphyll of the rhizome.

The prophyll, although the first structure to appear on the axillary growing point, does not elongate up through the confining base of its axillant leaf alone, but instead waits for the first true leaf which grows up within it. Measurements of a typical plant in process of elongating its shoots will show this synchronization.

TABLE II. PARTS OF A PLANT WHICH GROW AT THE SAME TIME

Position of leaf and sheath	Length in cm. of blade, sheath					
	Parent plant		Tiller sheath 1		Tiller sheath 2	
	Blade	Sheath	Blade	Sheath	Blade	Sheath
Last leaf	1.2*	0	.5*	0	.4*	0
Next to last	4.7	.9*	2.0	.5*	(prophyll .4*)	
2nd to last	2.7	6.0	(prophyll 2.5)			

* Indicates organs in process of elongating.

Here we see a repetition of a pattern of growth already discussed: that is, the simultaneous growth of a blade and its enclosing sheath. Although the prophyll does not exactly look like a sheath it seems to behave like one in most respects. It also bears a striking resemblance to the *coleoptile* or pre-leaf of a grass seedling (pl. 7, fig. 26) which accompanies the first true leaf of the germinating plant up through the soil and into the light. Both structures have two prominent veins and a pore at the top, are membranous, cylindrical, and have no blade. McCall (1934) has discussed this similarity in detail and has supplied anatomical evidence in support of the idea that the two organs are homologous.

Since no studies of the course of prophyll growth have been made and in view of the evidence that coleoptile and prophyll are basically similar, a growth curve (text-fig. 16) is reproduced from Weintraub and Price (1947) which probably

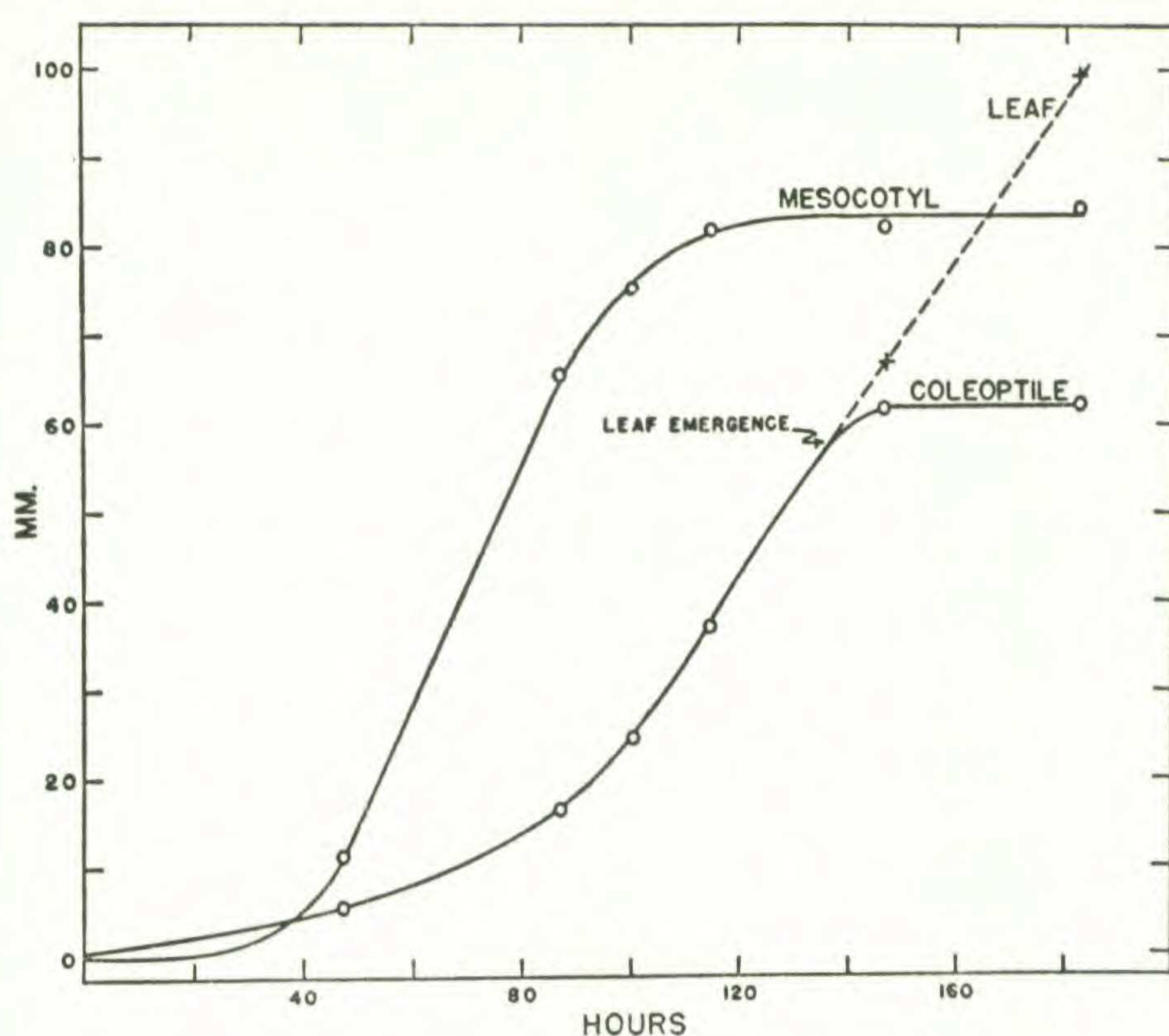


Fig. 16. Growth curves of the parts of a new oat seedling, in darkness at approximately 25° C. (From Weintraub and Price, 1947).

expresses fairly well the relationship of the pre-leaf and its enclosed true leaf. This curve represents the growth of the oat coleoptile and first leaf in the dark. It is observed that both structures have the same growth rate, and also that as soon as coleoptile growth stops, the leaf emerges. One must assume, therefore, that both structures began growing at approximately the same time unless some drastic change of leaf growth rate occurred, which is improbable. While this curve pertains specifically to the oat coleoptile, it undoubtedly applies roughly to the growth of the prophyll and the first leaf of an axillary bluegrass shoot.

It may be interesting to explain the presence of the third curve, labeled "mesocotyl" (text-fig. 16). The mesocotyl is an internode of the oat seedling which elongates upon germination and sends the growing point and the immature coleoptile up toward the soil surface. The curve shows this internode elongating before any of the leaves, which is not in keeping with previous statements to the effect that internodes elongate only after their associated leaf is fully developed. However, McCall (1934) in his examination of the oat seedling has shown that the so-called mesocotyl is the *first* internode and that another very short internode, the second, separates it from the coleoptile which can be thus considered the second leaf. The second internode does not elongate. Since the mesocotyl belongs to the first phytomer, it is under no obligation to wait for the coleoptile to elongate. The leaf of the first phytomer is minute and not readily visible. The basic system of phytomer development thus holds as true in the earliest stages of seedling growth as in more mature plants.

Growth of the Young Tiller.—Table II and text-fig. 15 show very well the interrelations between the parent shoot and the development of intravaginal branches. On a given phytomer the bud does not begin to grow into a tiller until the phytomer leaf has matured its blade and begun its sheath. Then four organs grow at the same time, the main sheath and the next main blade, the prophyll, and the first shoot leaf.

Since the prophyll and the shoot are thus synchronized, succeeding branch shoots are also synchronized. This accounts for the observation that in a sequence of intravaginal shoots on a plant, from the oldest to the youngest each shoot has one less leaf (text-fig. 17). There are exceptions to this of course. No one

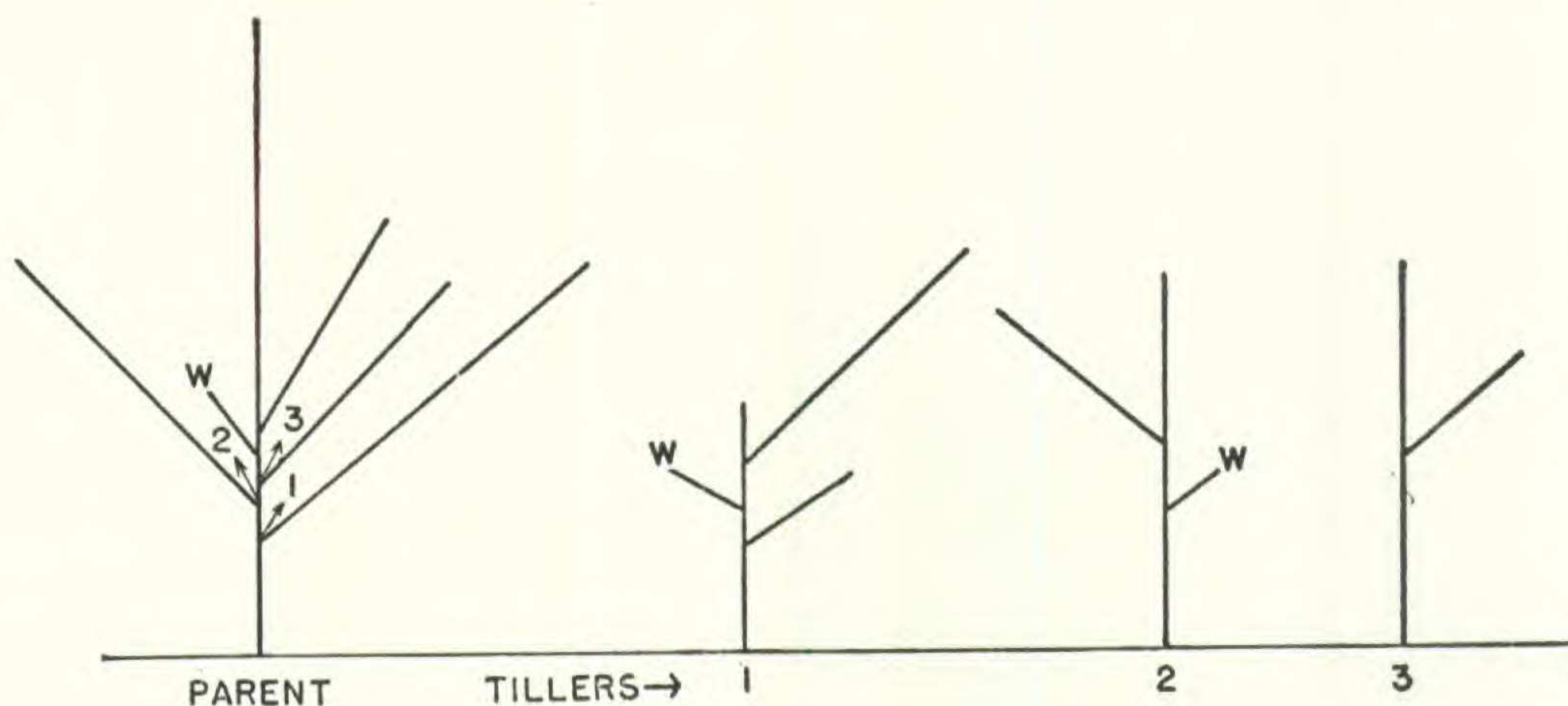


Fig. 17. On a plant which produces numerous tillers, each younger tiller is one leaf behind. W is short winter leaf.

phytomer seems to be wholly compelled to operate strictly in agreement at all times with its neighbors, though for shoots produced during the optimum tillering period in fall, under good conditions, such agreement seems commonly to exist. Under less favorable situations it is only reasonable to expect that a bud might hover between the decision to grow now and become a tiller or wait and grow up to be a rhizome. The indecisive individuals explain transitional types which are not strictly synchronized.

The prophyll may be longer but it is usually shorter than the leaf blade it encloses. In any case, the first sheath raises the first leaf out of the prophyll and exposes it to light. Other leaves of the shoot follow in the usual sequence, and the tiller becomes a new plant. Its own axillary buds can develop into other shoots in the same fall provided shooting starts early enough. Three generations are not uncommon and four or five are possible (pl. 9, fig. 28). Roots grow out from each mature node of the tiller crown and give it some measure of independence. In late spring any spare buds may develop into rhizomes. An inflorescence may appear the first spring though it is usually shorter and bears fewer leaves and spikelets than an inflorescence of the main axis. An intravaginal shoot with as few as two leaves can produce a panicle, while a rhizome with less than seven or eight leaves seldom flowers. This is in agreement with the observations of Cooper

and Saeed (1949) on ryegrass where a minimum of eight leaves are required before the main shoot will flower, while some tillers flower with only a prophyll.

Shoot vs. Leaf Width.—The above facts indicate that the flowering stimulus, once developed, can be transmitted from the main shoot to its tillers. To what extent other aspects of the growth of tiller and main shoot are interrelated is difficult to tell. Von Oettingen (1930), in a study of bluegrass leaf widths, stated that on rhizomes which have turned up there is usually a gradual increase in leaf blade width up to a certain point. Wherever an intravaginal shoot appeared, however, he found the leaf above to be abnormally narrow. This he attributed to a drain on the food resources of the main shoot by the branch. There are several reasons why such an explanation may not be altogether justified, though it is not so much with the idea of disproving his idea that the following discussion is presented as it is to demonstrate how information such as that included in this study may apply to a specific problem.

In the first place, as we have seen, the leaf blade on the main axis above a new tiller has practically reached its full development by the time the prophyll and the first leaf of the tiller start their elongation, so that one would expect any competition for food to influence the sheath above instead of the blade. It might also be added that bluegrass is an extraordinarily efficient plant and only a small amount of leaf would need be exposed to light for it to attain its independence. The enclosing leaves of winter are so short and limp that the new shoot reaches the light very soon after it starts to grow. Likewise, the first leaf is very small and would not consume extensive reserves in reaching its full extension. The efficiency of bluegrass in making maximum growth with a minimum of leaf and minimum consumption of stored carbohydrates or of accumulation of carbohydrates on a minimum of leaf has been suggested by data in Smelow (1937), Klapp (1938), Peterson (1946), and Harrison and Hodgson (1939) among many others.

Von Oettingen himself has indicated that reduced width is not correlated with a reduced number of vascular strands. In tillering varieties of sweet corn it has been shown that so-called suckers contribute to, rather than drain, food supplies of the parent (Jones et al, 1935). The explanation of Von Oettingen's observation is probably much more simple and points out the need for understanding not only the course of anatomical maturation but also the seasonal sequence of development of a plant to which statistical and taxonomic techniques are to be applied. The comparison made by Von Oettingen involved rhizomes which had no shoots and those which had only one or two. As a general rule, any rhizome which appears in fall will develop at least one or two side shoots, but those appearing in winter and spring are not apt to have any such shoots. The plants with branches thus go through a winter, and during that time leaf width of short-leaved plants decreases naturally (text-fig. 18). It is on these one or two late fall and winter phytomers that most of the branch shoots appear, and they are thus automatically associated with narrow leaves. Spring leaves are longer and wider and thus the contrast is accentuated. If, then, plants are later pulled up in summer at random

and the leaf widths examined, the significance of the narrowness of leaves associated with intravaginal shoots is not apparent.

Even the observation of a correlation between shoots and narrow leaves is open to some criticism. According to text-fig. 18, the relationship is actually just the reverse in rank meadow grass, where fall leaves increase in width while shoots increase in number. In grazed grass the early fall leaves increase in width while winter leaves become narrower. Shoots, meanwhile, increase in number all winter long, and virtually every new bud develops into a tiller. Therefore if the shoot had any effect on the leaf width it should show up in the average.

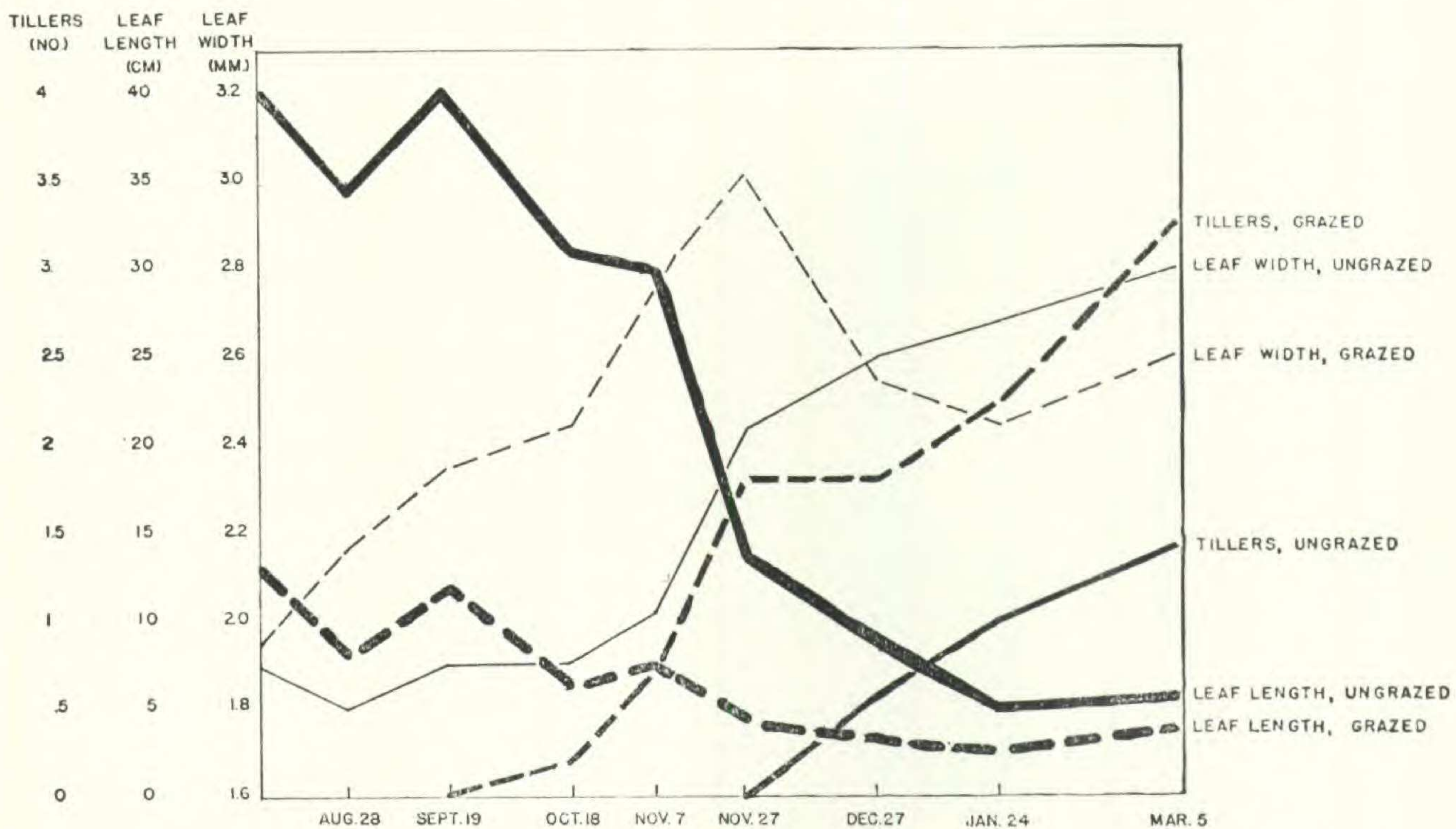


Fig. 18. Relationship of tillering, leaf length, and leaf width in meadow and pasture bluegrass in fall.

There are also indications that the severity of the winter and the seasonal development of available nitrogen in the soil influence the sequence of leaf widths. If the soil is frozen much of the winter, leaves will be deprived of water and will be narrower as a result. In mild winters such as that of 1949-1950, when the leaves were measured (text-fig. 18), very little freezing weather was encountered. One might thus expect that midwinter leaves of bluegrass grown in northern localities would consistently be narrower than those of southern-grown plants.

Shoot vs. Leaf Length.—While the relationship between leaf width and the presence of shoots does not seem to be constant, there is one correlation which seems to be rather consistent under normal cultural conditions: that is, the association of short leaf length with much tillering. This association is suggested in many ways. It is quite noticeable that mowing or grazing rank grass in early fall causes a great increase in the number of tillers. On unmown grass develop-

ment of shoots is weak and delayed until late fall or early winter. This difference is expressed the following spring in a much larger number of panicles in the mown grass (Spencer, 1949) and in the thickening of the early spring stand.

Some preliminary measurements of leaves on plants examined in late spring gave the following results:

Blade length	Number with shoots	Number without shoots
13-30 cm.	3	12
12- 3 cm.	27	5

More detailed data taken on grazed and ungrazed sods in fall and winter are compiled and presented in text-fig. 18, which shows clearly the delay of branching characteristic of ungrazed grass. This delay amounts to nearly two months, and the critical leaf length would seem to be around 10 or 12 cm., which is in keeping with the above figures. On grazed grass, however, leaves average under 12 cm. for most of the summer, but no shooting occurs until September. Leaf length alone is therefore not the deciding factor. We have thus defined the permissive and obligatory limits of shoot development. They can develop as early as late August, but seldom appear in quantity until October. By December they seem more or less obliged to appear.

The association between short blades and intravaginal shoots is further reflected by results obtained in some fertilization experiments made during different seasons. The fertilizer used was undiluted horse urine applied at the rate of two gallons to a square meter. Urine was used because of its quick action and its natural implications. The results are shown in the following table:

TABLE III
LEAF LENGTH AND NUMBER OF INTRAVAGINAL SHOOTS AS RELATED TO TIME OF
FERTILIZATION. (FIGURES REPRESENT AVERAGES OF 10 PLANTS
MEASURED ON JUNE 4, 1949)

Fertilizer applied	Number of branches	Leaf length of last complete leaf (cm.)
Late August	5.8	6.5
Late September	10.0	21.2
Late October	8.1	33.2
Early January	3.7	55.7
Early April	3.1	33.7
Control (no fert.)	3.6	15.0

Plants typical of the above experiment are shown in pl. 9, fig. 29. With a fall application a decided increase in shooting was observed so that in spring a large number of panicles were seen, but the numerous leaves were abnormally short. Winter applications yielded only slight increase in shoots and inflorescences, but the leaf was exceptionally long. The data for August show that again shortness of leaf is not infallibly followed by prolific branching. It emphasizes, instead, that probably no correlation holds true except under specific seasonal and environ-

mental conditions. The rhythm of the plant itself must be considered in interpreting measurements of this sort. In August, day length, soil moisture, and temperature are all quite different from those of September or October, and as already shown the plant is essentially incapable of forming shoots during that period. It is not strange that its response then should differ considerably from that a month or two later. There was little carry-over effect of the August application of urine because of a hot dry period during which much of the nitrogen was apparently lost. The extreme shortness of leaf in the August plants is not readily explainable, except for the possibility that the slight burning effect which the urine had on that occasion may have depleted the plants' reserves at a critical time. It has been observed that very close cutting or stripping of top growth at this period results in weak short-leaved plants.

Tillering in bluegrass has been shown to depend to some extent on day length (Evans, 1949; Harrison, 1934). Temperatures may also be a determining factor, for in the laboratory cultures with baby bottles it was found that while no shoots were produced with a 14-hour day at temperature of 70° F., at 40° numerous shoots appeared.

Shooting is thus seen to be a complicated activity. It depends on day length, temperature, nutrition, stage of development of the plant, and is associated with short leaves, though all short leaves do not produce shoots. Leaf width bears little if any relationship to shooting, except coincidentally.

Death of Shoots.—There is strong evidence that the parent plant may control the destiny of the tiller at certain critical points of development. This begins to be obvious at the time of elongation of the panicle, about the 10th to 20th of April in central Missouri (Table IV).

TABLE IV. DEATH OF INTRAVAGINAL SHOOTS IN SPRING

Date	Number of shoots examined	Number dead	Per cent dead
March 19	12	0	0
April 2	13	0	0
April 17	19	6	32
April 24	15	4	27
May 1	16	2	13
May 7	17	9	33
May 14	16	8	50
May 23	19	8	42
May 31	26	11	42

Dying of tillers is especially evident in rank, sod-bound, nitrogen-deficient grass which has not been grazed or mown, though it is probably also a common event wherever conditions are not ideal.

Death of some branches is a necessity in a sod which maintains a more or less even density from year to year, even though the average number of new vege-

tative shoots per plant is seldom more than two. The main shoot dies after bearing an inflorescence. Of the two tillers, one is generally dead before flowering is completed (Table IV). Perpetuation of the grass through the rest of the season is thus left up to the one remaining intravaginal shoot and whatever rhizomes develop during summer or fall. By early winter, however, practically all the original tillers have died, and it can be seen that maintenance of the population from one year to the next under meadow conditions is primarily dependent on the production of rhizomes. Rhizomes which develop in summer are primarily responsible for the inflorescences of the following year.

That the apparent detrimental effect which blooming has on the tiller may be related to water shortage is suggested by Sharman's statement (1947), that when the apices of the blind shoots (non-blooming tillers) of *Agropyron repens* are dissected during the flowering season they are "pliant and do not cut crisply, as though they were suffering from lack of water." As in bluegrass, these shoots of *Agropyron* generally die before the end of the year. It is also well known that grass crops such as maize require especially large quantities of water during the period of elongation of culms.

It would seem to be to the grazer's advantage to keep these tillers alive since they provide much of the summer's forage. By mowing at the proper time (about the third week in April) and by cutting low enough to catch the flowering head, blooming can be prevented and the vigor of the tillers might well be maintained. Unless these tillers live into the summer there may be a considerable loss of forage or sufficient thinning of the stand to permit invasion by weeds. Mowing at this stage of growth is not common in the United States, but Hamilton (1942) has mentioned that it is a practice on the intensively farmed ryegrass pastures of New Zealand, and suggests that were more power-mowing equipment available it might be profitably practiced more widely. Grazing at the proper time might also be used to serve the same purpose. Ryegrass, as Cooper and Saeed (1949) point out, is more of a problem, for usually a single cutting is not sufficient to prevent later flowering. Since bluegrass can only become "ripe to flower" during winter, one cutting is all that is necessary in that species.

Ahlgren (1938) has made tests simulating three conditions of spring-grazing, the first cutting of bluegrass being made: (1) to a 1½-inch level at a grass height of 4–5 inches; (2) when the head had just appeared; (3) after the head was mature. His data seem to substantiate the above conclusions, for making the cutting at the 4- to 5-inch height for a period of six years gave a progressively greater yield each year. Cutting at the time of appearance of the panicle was also consistently better than cutting at maturity. The data are reproduced below:

The 4- to 5-inch height just about coincides with the period when the panicle is starting to elongate. The specific time for mowing to best advantage can be determined by examining the heights of a few panicles while they are within the sheaths to see if the mower will cut them. It is quite possible that one of the more

subtle benefits of grazing a pasture involves the prevention of heading at an early stage, and thus the encouragement of the tillers which must take the plant through the summer.

TABLE V
PERCENTAGE YIELD OF KENTUCKY BLUEGRASS FROM PLATS GIVEN VARIOUS CUTTING AND FERTILIZATION TREATMENTS. (FROM AHLGREN, 1938)

Year	Complete fertilization			No fertilization		
	4-5 inches	Early heading	Fully headed to mature	4-5 inches	Early heading	Fully headed to mature
	%	%	%	%	%	%
1932	79	123	100	71	93	100
1933	92	97	100	74	81	100
1934	113	103	100	108	101	100
1935	108.2	108.2	100	118.8	110.8	100
1936	143.6	105.4	100	189.8	136.7	100

THE FLOWERING SHOOT

Purpose and Design.—Bluegrass must be appreciated more for the delicate and effective way in which it presents its small flowers to the wind than for the beauty of the individual flower. There may be from 100 to 1000 flowers, or *florets* as they are called in grasses, on each flowering shoot. Considering that the plant has only the phytomer to build with, it does a very efficient job of display. By elimination or reduction of all unnecessary structures including blades, sheaths, roots, and some buds, a flowering shoot of quite simple design is achieved. This shoot consists of a main stem or *culm* which holds a branched pyramidal inflorescence or *panicle* well above the ground (text-figs. 3 and 20). Clusters of florets (called spikelets) depend from the tips of the panicle branches. The average culm is merely a portion of the vegetative axis which has been obliged, because of the initiation of an inflorescence at its growing point, to follow a course of development different from that of non-flowering shoots. It is distinctive chiefly in having long internodes, reduced leaves, no buds or roots, and a hollow stem, all of which indicate the strong economies of material put into force when the plant is called upon to flower.

The average culm consists of a series of 3, 4, or 5 phytomers, with each higher one being less like the normal vegetative ones at the base of the plant. For convenience the standard number of phytomers will be considered as 4, and will be numbered from the lowest, least elongate (1) up to the highest and longest (4). Actually there is no specific phytomer at the base which one can designate as belonging to the flowering shoot rather than to the vegetative shoot from which

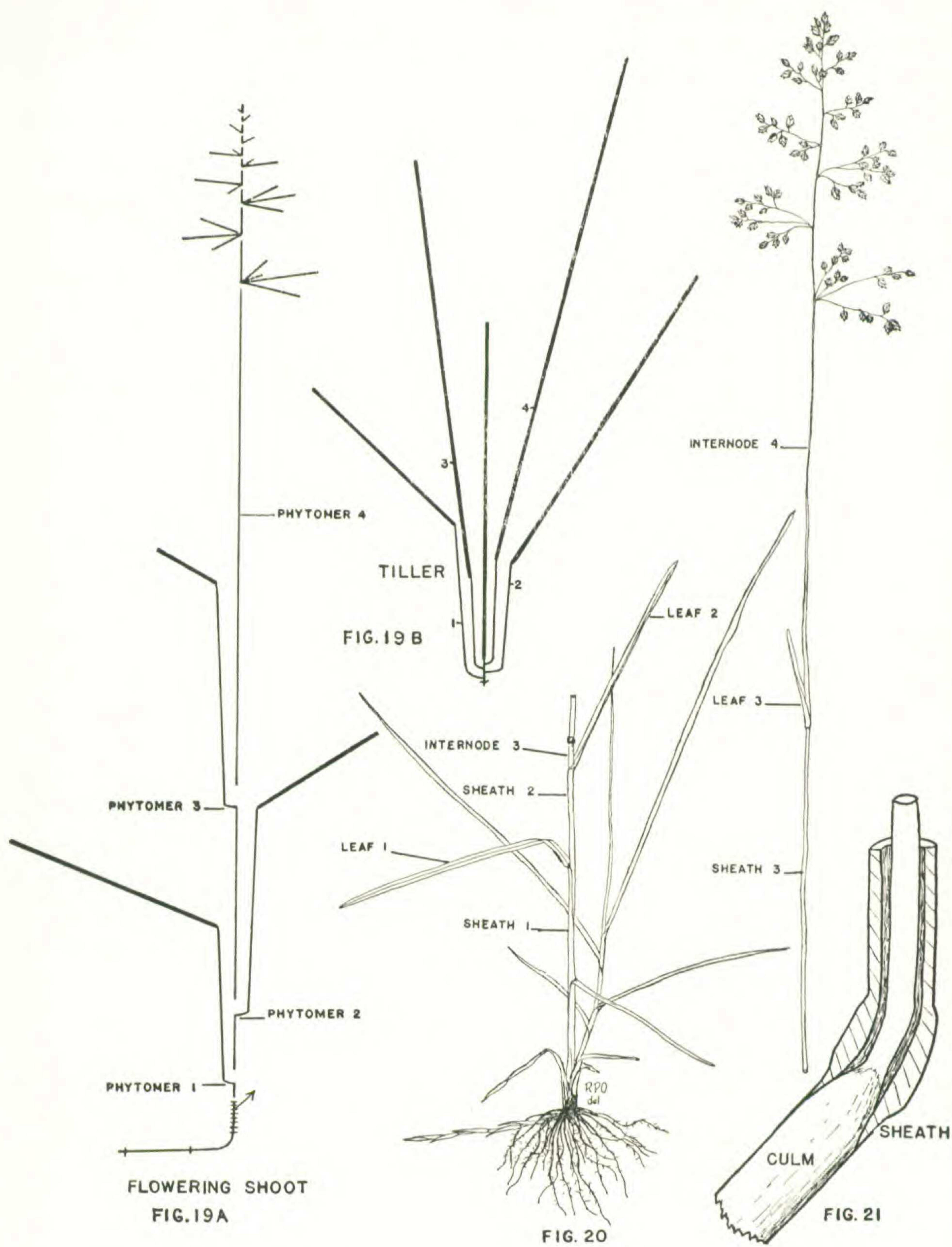


Fig. 19. Diagram of a typical flowering shoot (A), and one of its tillers (B).

Fig. 20. Bluegrass plant from an old meadow showing an average flowering shoot.

Fig. 21. A fallen flowering shoot is straightened by the development of tissue on the lower side of the enclosing sheath.

it springs, for the transition is not always abrupt. Each of these culm phytomers is a distinctive combination of different internode, blade, and sheath lengths (text-fig. 19A). In an old unmowed, ungrazed, unfertilized, unirrigated, unshaded stand of Missouri bluegrass the lengths of successive internodes will increase toward the panicle in a rough ratio of 1, 4, 12, 30. The panicle on top would then be about 9 cm. Each of these internodes, except the last, bears a sheath at its top which in turn bears a blade. The average sheath lengths in centimeters would be about 9, 12, 13 and 0. The leaf blade lengths are in reverse order to the internodes for they average 13, 9, 4 and 0. We thus can draw the following thumbnail arithmetical sketch of the flowering shoot:

TABLE VI
COMPARISON OF LENGTHS (IN CM.) OF FOUR SUCCESSIVE *CULM* PHYTOMERS WITH THOSE ON A SUCCESSION OF FOUR *VEGETATIVE* PHYTOMERS ON ASSOCIATED TILLERS. (SEE TEXT-FIG. 19 A & B)

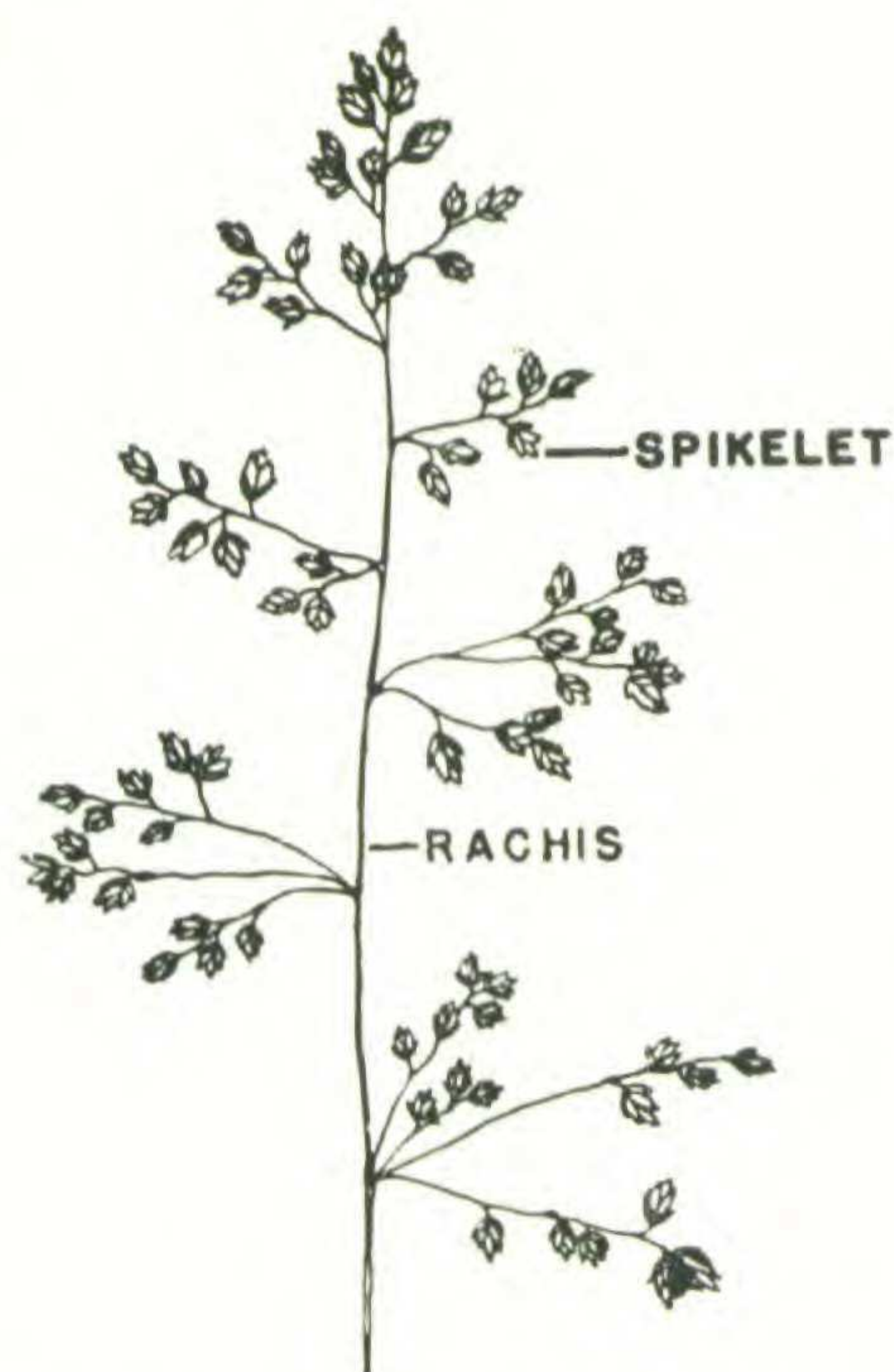
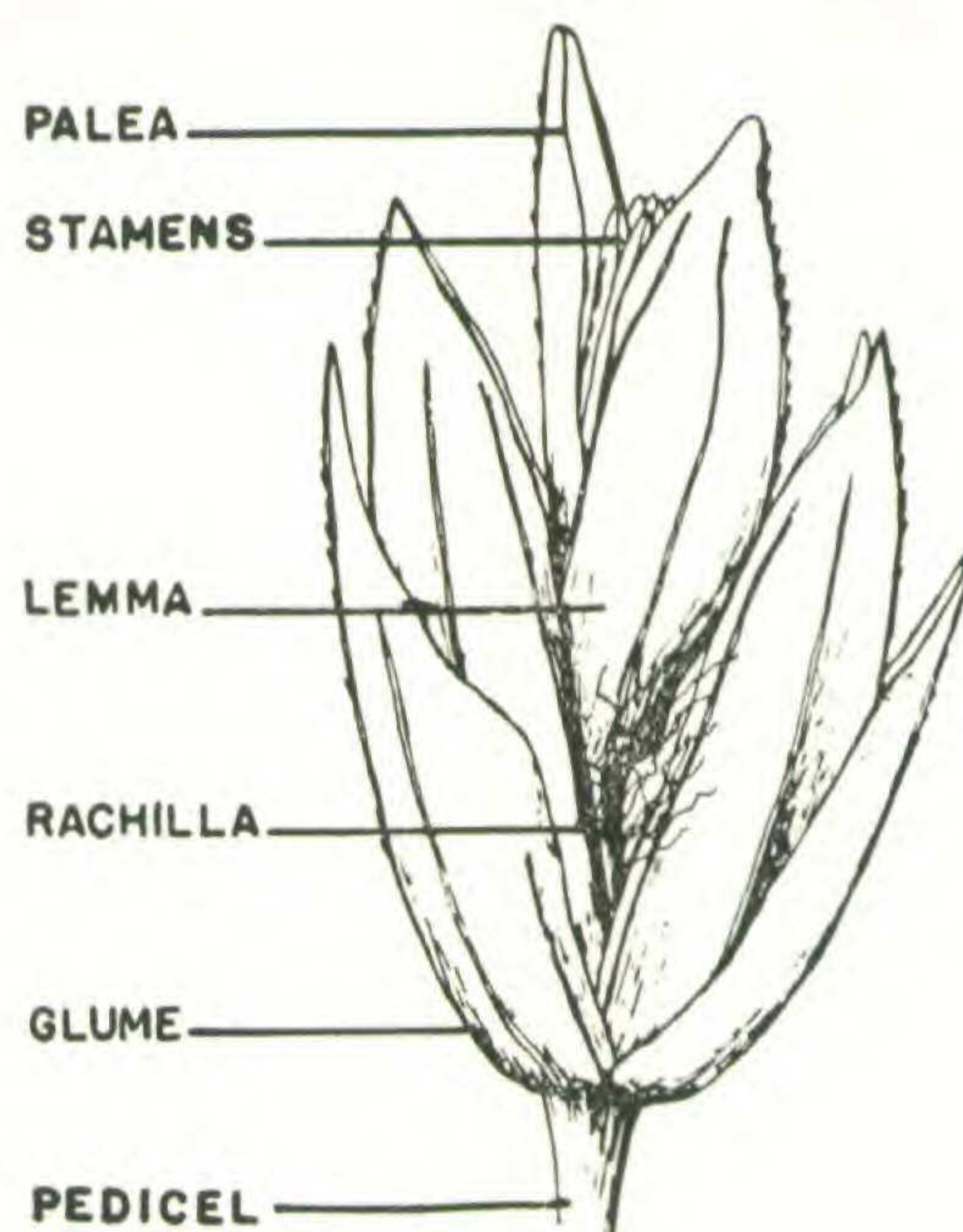
	Culm phytomer					Vegetative phytomer			
	1	2	3	4	Pan- icle	1	2	3	4
Internodes	1	4	12	30	9	—*	—	—	—
Sheaths	9	12	13	0	0	8	6	5	6
Blades	13	9	4	0	0	12	20	24	30
Total leaf	22	21	17	0	0	20	26	29	36
Date leaf completed	Apr. 12	Apr. 17	Apr. 26			Apr. 12	Apr. 26	May 16	June 15

* Vegetative internodes too small to be measured.

The last sheath immediately below the panicle may appear as a small hook or scale at the top of the last phytomer. Rarely a complete leaf may be found. These figures give only a general picture of the culm, and it is not intended to suggest that they pertain to other strains or plants from other habitats. The first phytomer is seen to have a very short internode and a long leaf blade while the last phytomer has a long internode and no leaf at all. The first leaf is not greatly different so far as blade and sheath length are concerned from its vegetative contemporaries (text-fig. 19B, No. 1). With the second blade, however, the influence of the developing panicle is evident, for comparable vegetative blades average 10 cm. longer than those on flowering shoots.

Culm leaves are consistently broader than the contemporary leaves of associated vegetative shoots. Thus measurements of the last leaves on 48 plants, 24 with inflorescences and 24 without, showed on April 21 average widths of 3.4 and 2.3 mm. respectively. On May 1, after the last culm leaf had appeared the difference was 2.7 and 2.3 respectively. This indicates that the *last* culm leaf is less wide than its predecessors. In general, there is little difference in the width of the first two culm leaves.

The internodes of the bluegrass culm are rather delicate structures which would soon fall to the ground were they not partly encased by strengthening sheaths.

Fig. 22. A bluegrass panicle, $\times \frac{4}{5}$.Fig. 23. A bluegrass spikelet, $\times 16$.

The lowest two internodes are usually completely hidden from view while the third generally shows only a few centimeters at the top. The last internode is sheathed about half way up. The degree of overlap varies radically from plant to plant.

In case the bluegrass culm, while elongating, happens to fall to the ground as a result of wind, rain, or trampling, a rapid reaction takes place in the vicinity of one or more of the nodes causing development of tissue on the lower side of the culm which gradually restores at least a part of its perpendicularity. On close examination it will be found that in bluegrass the actual growth and straightening process depends more on the basal part of the sheath than on the internode (text-fig. 21). This sheath builds up a wedge-shaped accumulation of tissue around its lower side, which as it bends up, forces the delicate culm within to raise also. Arber (1934) states that in other species of grass such straightening may involve only the sheath, as in bluegrass, or both sheath and internode, or internode alone. The bluegrass internode, whether on the culm or the rhizome, apparently has very little to say about what position it will assume.

The Panicle.—At the summit of the culm is the panicle or inflorescence (text-fig. 22). The branches of this panicle, which arise at nodes, are grouped together in successive fan-shaped tiers inserted alternately on the panicle axis. Since the branches of the lower tiers are longer than those of the upper ones the outline of the inflorescence is somewhat pyramidal. There are from three to five branches at each of the lower three or four nodes, and these are almost perpendicular to the main axis at flowering time though in some strains they may droop or be appressed to the panicle axis. The spikelets, or flower clusters of the grass, are borne at the tips of these branches and of their subsidiaries.

The panicle axis, or *rachis* as it is sometimes called, is a continuation of the culm. It is composed of some eight or more internodes, only the lower ones being very prominent. This contrasts with the culm internodes which decrease in length toward the base of the plant. There are no leaves on the rachis phytomers.

Beginnings of the Flowering Shoot.—A flowering shoot is a sudden, striking thing and seems so different that it sometimes prevents us from understanding its relation to the course of development in the rest of the plant. In bluegrass the initiation of the flower takes place in the cold weather of late fall and early winter, and thus development is slow and goes unnoticed. In spite of its early start, bluegrass does not display its flowers until mid-May in Missouri. Cold weather and short days have no magic in themselves, and can work only through the physiological systems of the plant. Under fall conditions it has been shown (Buckner and Henry, 1945; Peterson, 1946) that bluegrass carbohydrate reserves rapidly reach a peak. In general, such accumulation of carbohydrates seems to be one of the significant factors leading to the "ripe to flower" condition in grasses. That other systems play a part goes without saying, but no effort will be made here to fathom the chemical complexities associated with the inception of flowering shoots.

To trace the development of a vegetative shoot into an inflorescence we shall have to go back to the growing point, for that is the beginning of everything. Musgrave (1940), Nishimura (1923), and Evans (1949) have given good accounts of this process. The following description attempts to synthesize the work of these three authors.

The vegetative growing point runs on a rather close margin. It commonly has only three or four phytomer primordia differentiated and available for use (see pl. 5, fig. 13). As the plant approaches fall, however, either the phytomer organs differentiate less rapidly, or else new primordia are cut off from the growing point at an increasing rate, or both, for incipient phytomers begin to accumulate and as a result the blunt rounded vegetative growing tip of the youthful shoot becomes a longer, rather conical, wrinkled, translucent point (pl. 8A). This is a tendency which precedes inflorescence development in practically all grasses, although the number of phytomers accumulated on the point and its actual length may vary greatly with different species.

Protuberances Appear.—The lower, old phytomers of this new cone appear normal enough, and bear the usual leaf primordium at their upper end, but toward the point, on the younger primordia, there may be only a faint ridge or no sign of a potential leaf. Then something happens. The deadline is up, and all phytomers which have not formed leaf primordia are obliged to get along without them, for the reproductive phase has begun. The first visible sign of this event on the growing point is the appearance of small knobby protuberances which, though arising in a similar alternate manner, are obviously different in origin from the crescentic ridges from which leaves arise (text-fig. 24A; pl. 8B). These shining protuberances appear first on those phytomers which have only the faintest trace of a leaf ridge, then soon both *below* and *above*. The protuberance is a rather

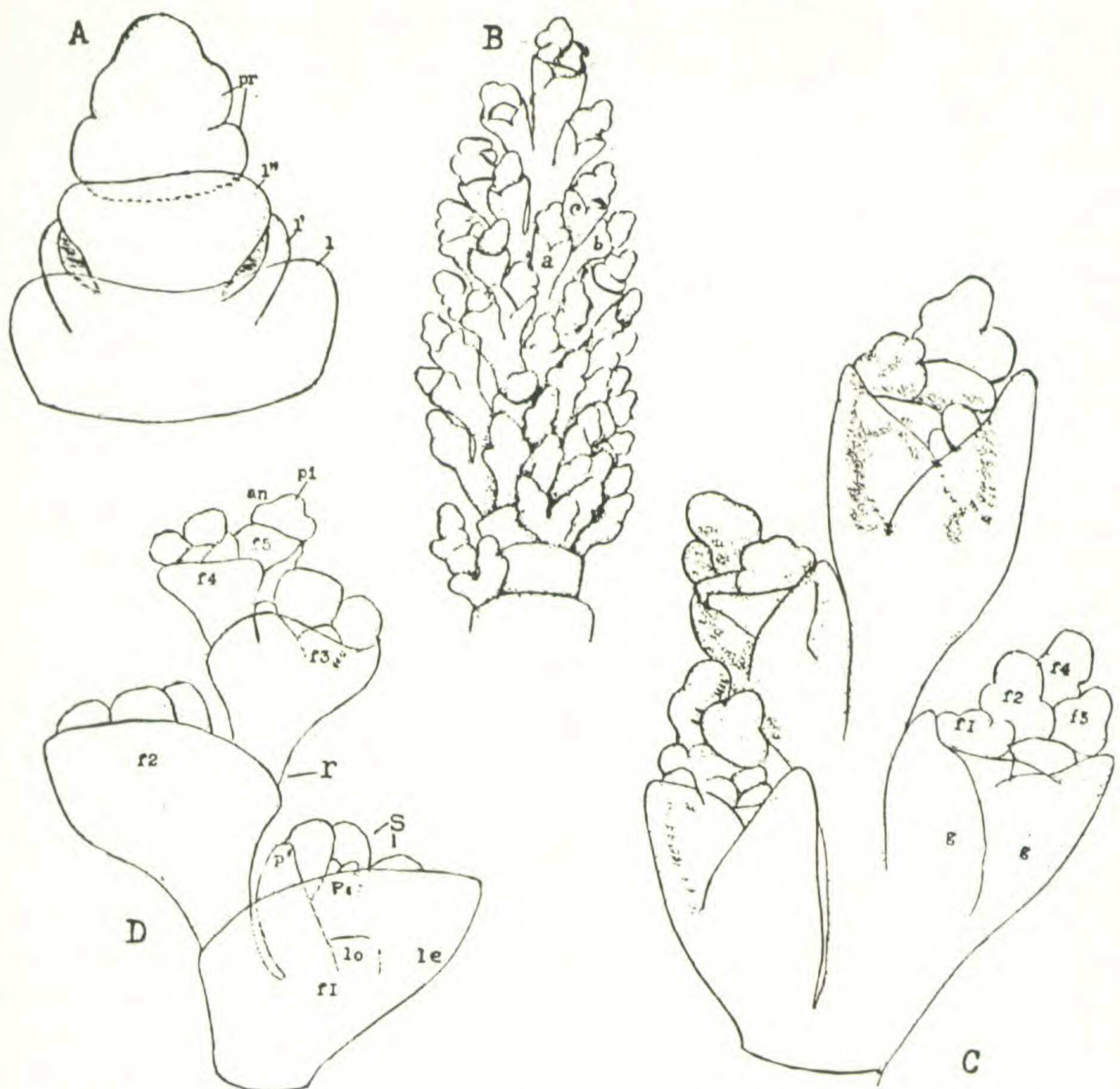


Fig. 24. Drawings from Nishimura (1923) showing details of panicle and spikelet development: A, the elongate growing point which anticipates panicle development; B, small ridges begin to appear on the advanced protuberances and foretell development of glumes; C, a panicle branch holding several developing spikelets; D, a much-enlarged individual spikelet with glumes removed and showing beginning of development of florets and reproductive parts; *pr*, protuberance; *l*, *l'*, *l''*, successive leaf primordia; *g*, glume; *f1*, *f2*, etc., successive florets; *an*, stamen primordium; *pi*, pistil primordium; *r*, rachilla; *p'*, palea; *lo*, lodicule; *s*, stamen.

unique development for, although it obviously represents a branch of the main axis, it is the only time during the growth of a grass that a growing point is not encased in its own sheathing cone of leaves. Here is a phytomer which consists of nothing but stem. Through continued cell division it grows very slowly, almost as though it were a root. The one phytomeric function which it seems to retain is the ability to branch. Thus after about a month secondary protuberances arise (pl. 8C), and in another month tertiary ones appear. By this time most of the winter has passed, and in late March the growing point may still be only about 1.5 mm. long and yet will contain practically all the cells necessary to build the entire skeleton of the mature panicle.

The Development of Spikelets.—In April on all the naked ends of protuberances of all orders small crescentric ridges begin to appear (text-fig. 24B). Just as in

the main vegetative point, these ridges are alternately arranged and later develop into minute leaf-like structures. Thus the conventional phytomer consisting of a leaf and an internode is reestablished. This is the beginning of the bluegrass spikelet, or flower cluster (pl. 8D; text-fig. 24C). The first signs of spikelet development appear on those protuberances located somewhere between the middle and upper third of the panicle, and the spikelets at the tips of the *main* branches develop before those on subsidiary branches.

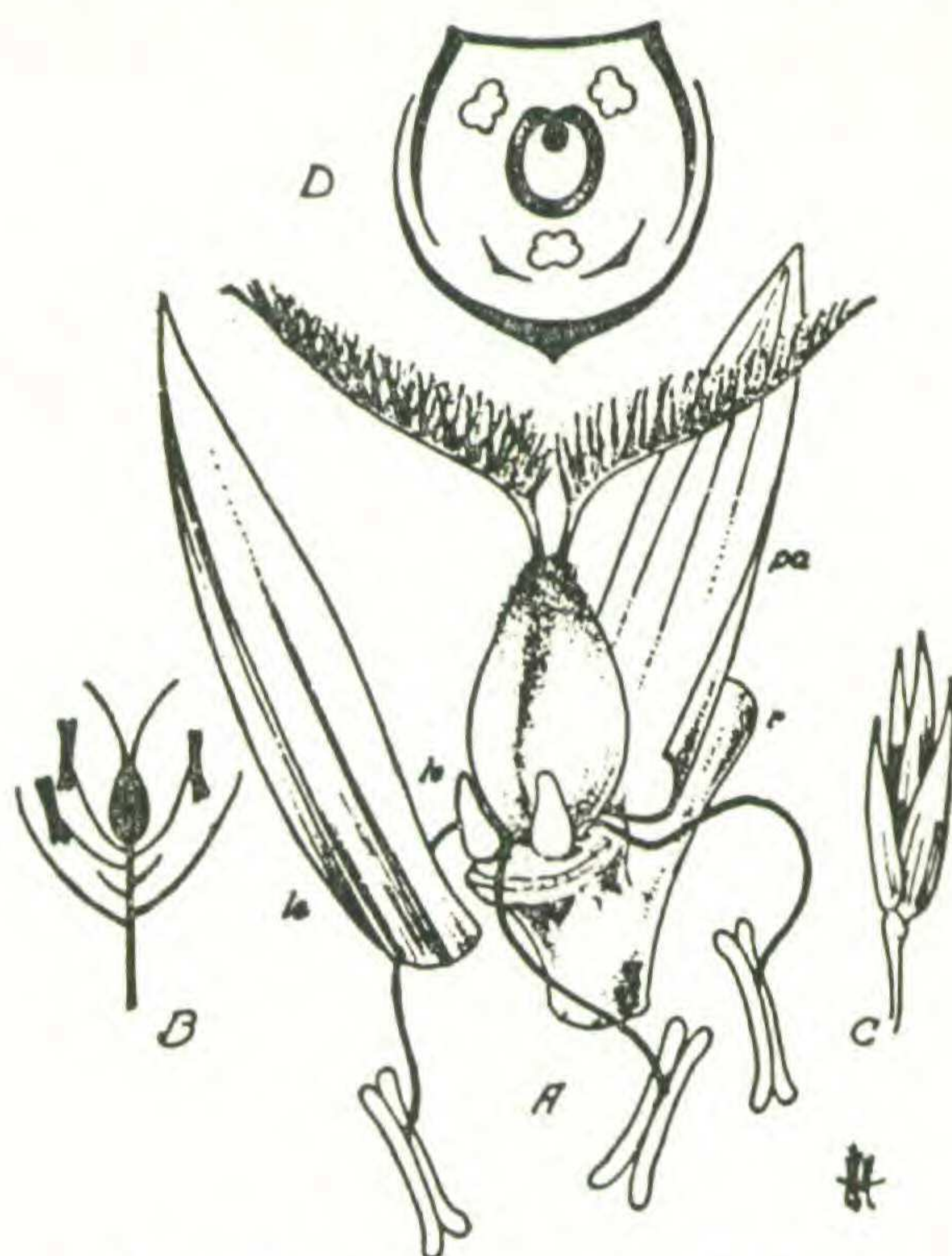
The first two leaf-like structures which develop from these primordia are called *glumes*. They are only 2 or 3 mm. in length when mature, and completely enclose the growing point and its developing structures. Once conceived, the two glumes elongate more or less simultaneously, which is not exactly in keeping with the usual sequence of phytomer development. As shown in text-fig. 26, the last two blades and then the last two sheaths of the culm elongate simultaneously, so that apparently when the growing point is going into or coming out of the phase of panicle formation the normal sequence of elongation is somewhat altered.

Before the glumes close over the growing point a series of 3–5 phytomers with leaf primordia have begun to form (text-fig. 24C; pl. 8E). These primordia elongate gradually after the glumes enclose them. They are called *lemmas*, and they are distinguished from the lower glumes because they bear, in their axils, an axillary bud which will soon develop into that long-awaited-for phenomenon, the floret (text-fig. 24D).⁴ Differentiation of successive lemmas and florets progresses from the base of the spikelet toward the tip.

As with most axillary buds, the first structure produced from the floret bud is a membranous, two-veined, compressed sheath-like organ which, though not called a prophyll any longer, very much resembles one. It is dignified by the name *palea*. The growing point of the floret bud (text-fig. 24D), then proceeds with the differentiation of the critical flower parts, producing in turn three stamens from small papillae just below the growing point, the pistil from a crescentic protuberance very much resembling a leaf primordium, and finally the two styles and stigmas from papillae on the pistil (text-fig. 25). The ovule or egg sac, which is perhaps the final leaf primordium, remains short inside the pistil after that structure has closed around it. Within it will develop the egg cell, which would appear to be the arrested growing point.

From four to seven phytomers are ordinarily found in a bluegrass spikelet. Their leaves are the glumes and lemmas, their axillary buds are the florets, and their minute internodes join together to form the spikelet axis or rachilla (text-fig. 25). The transition toward termination of the growth of this axis is usually expressed in the form of a final much-reduced phytomer which consists of a fragile internode and a minute lemma, the so-called sterile floret.

⁴By following the phytomer concept to the end and assuming that the glumes are homologous with sheaths or blades, we should, in reality, recognize the first three leaves (two glumes and the first lemma) as glumes instead of just the first two, since the first floret is a bud at the base of the fourth spikelet phytomer, and thus belongs to the fourth leaf, not the third, which is therefore "sterile." This is a technicality of no great importance to the matter at hand, and might cause considerable confusion among grass taxonomists. That there are no hard-and-fast rules in this respect is illustrated by the observations of Sharman (1947) that florets are sometimes found in the axils of the glumes.



A, flower of a grass (schematic); *lo*, lodicules; *r*, rachilla; *le*, lemma; *pa*, palea; B, longitudinal diagram of flower; C, spikelet; D, floral diagram.

Fig. 25. A diagrammatic sketch of a typical grass flower. (From fig. 429, on p. 627, of Johnson's "Taxonomy of the Flowering Plants," 1931. Reproduced by permission of the Century Co., Publishers).

Elongation of Panicle and Internodes.—As the process of spikelet differentiation proceeds in early April, it seems to send a pulse of life down through all the phytomers which have been biding their time since being inhibited when the proliferating urge assumed control months before. Their internodes begin to elongate. The actual processes involved in this revival of growth are shown in text-fig. 26. The initial quickening is limited to the panicle proper. Growth is slow at first, less than 1 cm. between March 27 and April 12, then it increases rapidly during the next ten days to full length. It may not be altogether a coincidence that this panicle elongation comes immediately after the first and second leaves of the culm have matured. It suggests that some inhibition may be involved.

Not until the panicle has reached its mature length do the internodes of the culm begin to elongate to any extent. An exception to this is the first short internode, which begins to lengthen several weeks before the panicle matures. This course of growth seems slightly different from that characteristic of wheat as shown in text-fig. 6. In wheat the growing point at the beginning of the protuberance stage has had more phytomers and culm development is more drawn out and deliberate, with each successive internode behaving as an individual. The result is a culm with more joints of more nearly equal length. Maize is a more extreme example of this same situation. Bluegrass with its short growing point presents only four internodes, only three of which reach any considerable length.

It is a common observation that in wheat, corn (Sharman, 1942), and rye (Prat, 1935) the last two internodes elongate at the same time. Prat attributed this to the fact that there is no leaf on the last phytomer, therefore, the internode does not have to wait to begin its growth. The fact that in the bluegrass strain examined here the last *three* internodes grow at the same time is probably related to the absence of the last blade and the shortness of the third one.

Culm Leaves.—While it is usually considered that the bluegrass plant lies dormant during winter except for inflorescence initiation, it is actually producing a certain amount of leaf growth. On shoots destined to flower, no new leaf primordia are produced once proliferation takes place, but those primordia already completely formed do follow a normal course of development within the limits of environmental factors. The number of leaves which thus develop during the coldest weather is usually only two or three and these are very short (text-fig 26WB). The internodes below these winter leaves do not elongate, for they are apparently mature by the time spikelets begin to differentiate in spring. These leaves differ little, if at all, from comparable leaves on vegetative plants or on tillers of the same plant.

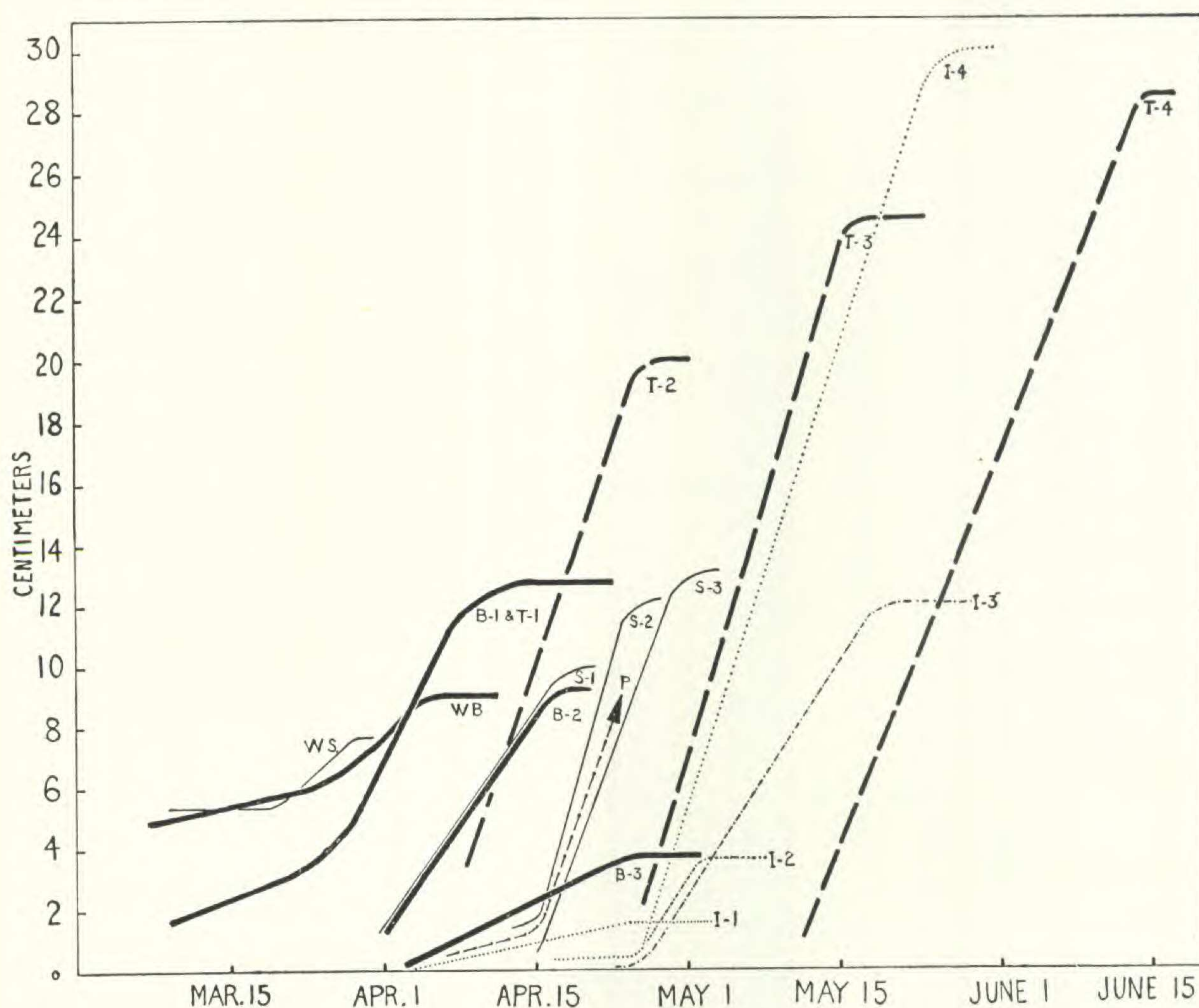


Fig. 26. Curves of growth made by various organs of meadow bluegrass during the period of flower-shoot development in spring.

With the approach of warmer weather in late March leaf growth receives an impetus and new leaves grow longer. The last true winter leaf and the first culm blade apparently respond, rather abruptly, to the rise in temperature. (See sheath WS and blade WB and B-1 in text-fig. 26.) The first blade on the culm continues elongating. By early April it is joined by *leaf blades 2 and 3* and *sheath I*, which elongate at the same time. When these mature, *sheaths 2 and 3* and the panicle elongate almost simultaneously. Immediately upon their maturation, *internodes 2, 3, and 4* begin to grow. This rush of growth is in decided contrast to the deliberate growth of phytomers on vegetative shoots of the same plant where only one blade and one sheath elongate at the same time and the internodes do not elongate at all. This speeding up of the development of phytomers immediately below the inflorescence has been noticed by Sharman in maize (1942) and in quack grass (1947) and is suggested by data of Prat (1935) for rye. This is one of the factors involved in the rapid appearance, in spring, of a large number of leaves in a very short time. The more flower shoots there are the more vigorous this spring flush will be.

There is an interesting contrast between culm and vegetative leaves with respect to final length and rate of growth. Up until about the last of March the growth rate of the two types of leaves is very similar. After that each successive culm leaf elongates less rapidly and is successively shorter (text-fig. 26, leaves B-1, B-2 and B-3). Tiller leaves (T-1 to T-4), on the contrary, elongate somewhat more rapidly, and become successively longer even though on the same plant. This would suggest that if the developing panicle has any effect on leaf growth, it is not transmitted to the leaves of intravaginal shoots as the stimulus for flowering apparently can be. More probably, the shortening of culm leaves is not an inhibitory effect at all, but dates back to the time when the growing point first changed in the direction of flowering. Leaf primordia were stopped in their tracks and consequently when an opportunity came the following spring to elongate there were successively fewer cells in each younger primordium available for elongation.

The absence of buds on the culm is also probably due in part to the fact that their formation was interrupted by the inception of panicle development. Sharman (1947) commented on the absence of buds on the culm of certain species, stating that microdissection showed that early stages of bud formation did take place. The failure of the bud to develop further he attributed to the effect of elongation in pulling the tissues of the bud apart. This seems improbable in view of the presence of well-developed buds on the phytomers of rhizomes which have long internodes. The influence of the developing panicle in suppressing further growth is probably of more significance.

The reason for suppression of roots on culm phytomers is even less clear. In part, it may merely be that the culm internodes do not come close enough to an adequate rooting medium. Roots have been seen on culm phytomers as far ad-

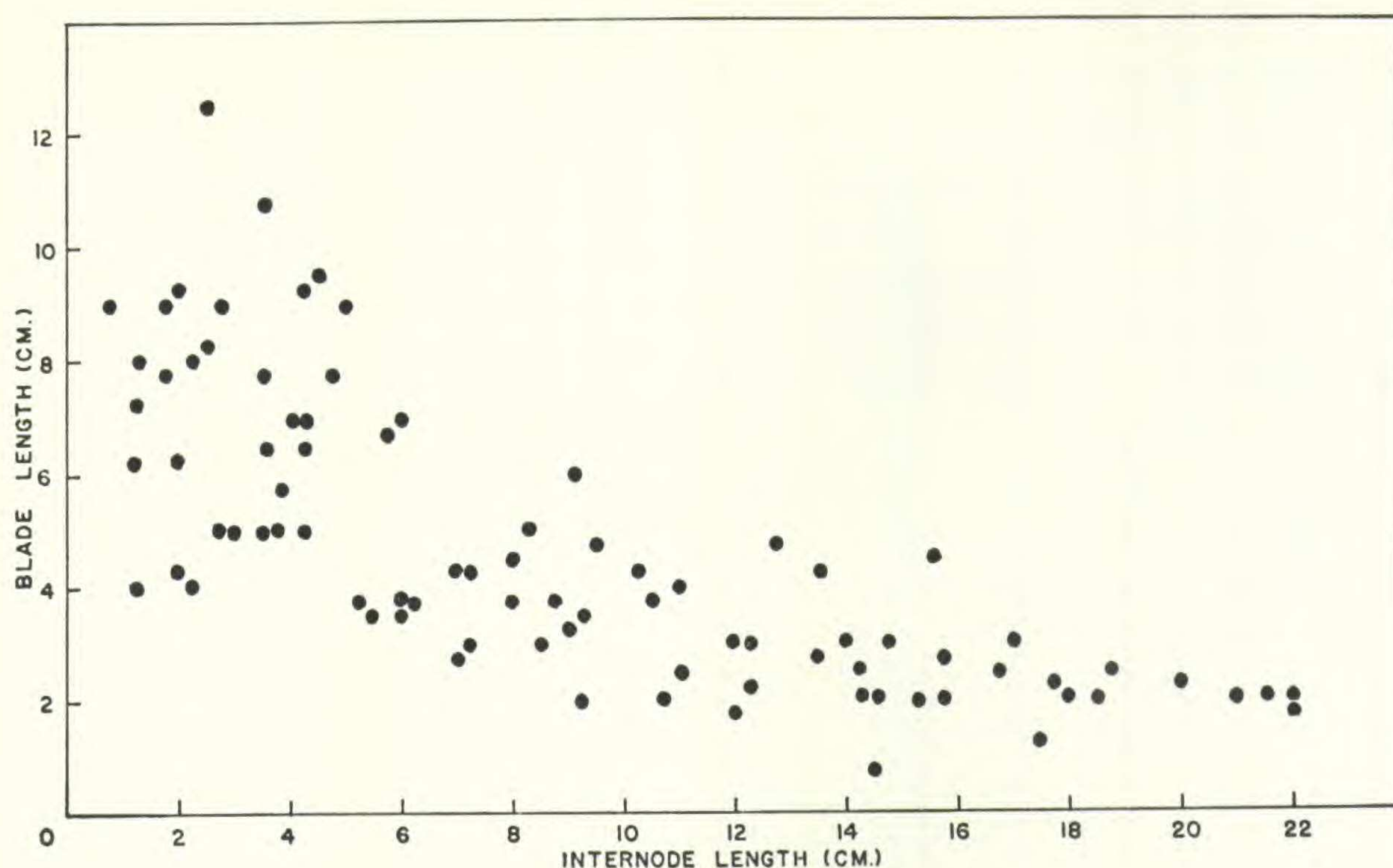


Fig. 27. The relationship between length of phytomer internode and phytomer leaf on the culm of bluegrass. Plants were from various meadow habitats.

vanced as No. 3, under conditions where the nodal region was exposed to moisture and darkness.

The relationship of short leaves and long internodes in the upper part of the culm is apparently more than mere coincidence. Although the shortness of the leaf may be explained on a historical basis, the long internode probably involves other factors. It has been mentioned in connection with the rhizome that the internodes of phytomers whose leaves turn up and reach the light are inhibited. If the leaf does not reach the light then the internode elongates. Many other observations indicate that the bright light inhibits the elongation of internodes, while in the dark or shade elongation can take place. It is probable that the shortness of the culm leaves reduces their inhibiting action at the same time that the developing inflorescence is producing auxin in quantity (Prat, 1935). Thus both conditions appear to favor increased internode length. The relationship between leaf and internode length on the culms of bluegrass from a variety of habitats is shown in text-fig. 27. As further evidence for the validity of this relationship, it has already been mentioned that the last internode, devoid of any leaf, is by far the longest. Also suggestive is the fact that very little elongation of the second, third, and fourth internodes takes place until the last leaf has reached almost its full extension. Unfortunately, the panicle reaches its final length about the same time, so that there is no way of determining which is the more significant releasing factor.

LEAF GROWTH IN RELATION TO SEASON AND ENVIRONMENT

Day Length, Temperature, and Growth Rate.—The casual observer probably realizes that bluegrass begins to green up in early spring, blooms in May, and gets tall and somewhat brownish in summer, then greens again in early fall and turns brown again in December. This sequence of events seems quite regular year after year. Weather variations induce only moderate fluctuations. One would gather from this that the bluegrass plant has a way of knowing what time of the year it is. Apparently that knowledge is conveyed largely through the medium of day length and temperature.

Evans and Watkins (1939), Evans (1949), and Peterson and Loomis (1949) have described the influence of various changes of day length on bluegrass. The chief conclusions reached are that leaf length and tillering can be controlled by day length, though temperature may affect the leaf length to some extent at any given day length. The results of Peterson and Loomis' experiments are indicated below:

AVERAGE LEAF LENGTHS

Temperature	Day length	
	11 hrs.	19 hrs.
56° – 65° F.	9 cm.	15 cm.
61° – 75° F.	16 cm.	25 cm.

Day length has been widely studied because its control is so easy under experimental conditions, but it is only one factor among many which affect the efficiency and consequently the behaviour of bluegrass. Over its full range, temperature can exert just as profound an influence. Thus Darrow (1939) has found that "plants grown at temperatures of 59° F., 77° F., and 95° F. produced at 59° a tall succulent bushy top growth with many leaves and at 95° an erect, non-succulent, short top growth with few leaves." Brown (1939) found that under controlled conditions maximum top growth was produced at temperatures between 80 and 90° F. when plants were clipped monthly. He also found that 50 degrees was the critical mean below which very little top growth took place in established sod, but that in new seedlings production was large at an average soil temperature of only 44° F.

In the series of experiments where bluegrass was grown in baby-bottles, the plants were first placed under temperatures ranging from 70° to 75° F. They were later moved to a room kept at 40° F. In the beginning the day length was 14 hours; the humidity was not controlled. Measurements of the growth of individual leaves were made weekly. Average growth rates and leaf lengths are recorded in Table VII.

TABLE VII

Month	Period	Growth per day in cm.	Length of youngest mature leaf in cm. (Average of 12 plants for two periods)	
Nov.	25-30	1.7 }	7.5	14 hrs at 70° F. Av. = 1.78 cm.
	30- 7	2.43 }		
Dec.	7-15	.94 }	15.0	
	15-25	1.88 }		
	25- 3	2.07 }	27.0	
	3-12	1.64 }		
Jan.	12- 3	.38 }	23.0	
	3- 9	.67 }		
Feb.	9-16	.48 }	25.5	
	16-22	.34 }		
	22- 1	.17 }	15.0	
	1-15	.47 }		
Mar.	15-22	.43 }	9.0	
	22-29	.35 }		
	29- 5	.25 }	7.9	
	5-12	.20 }		
Apr.				Temperature up to 70° F. on the 17th
	12-19	1.07	8.2	

It can be seen that the growth rate became much slower and the leaves gradually much shorter after the plants were placed under the low temperatures. In general, the growing period of a given leaf remained about the same and consequently initiation of new leaves was not greatly retarded. Tillers were not found on any of the plants while they were kept at the high temperatures, but when plants were transferred to low temperatures tillers soon appeared and the leaves became a deeper green. These are changes very similar to those occasioned by growing bluegrass under long and then short day-lengths. Five weeks before the end of the experiment the day length was changed to 12 hours while the temperature remained at 40° F. This change had only a slight effect on succeeding growth rates. During the final week, through failure of the cooling equipment, the temperature went up to 70° F., and did not come down for several days. This resulted in a striking increase in growth rate for that week.

Growth Rates in the Field.—Approximate growth rates of bluegrass leaves under natural conditions throughout the year were calculated from two sources of data. For vegetative leaves appearing in March, April, and May, data collected in connection with the development of the tillers on the flowering shoot have been used. Since all tillers produce very short winter leaves, and then begin with surprising coordination to produce longer spring leaves about the same time, and at the same rate, successive leaves fall into definite length classes which remain fairly distinct for the first 4 or 5 leaves of new growth. It is from averages of 10 leaves of the same class that the curves are made. Dissection of the shoot was

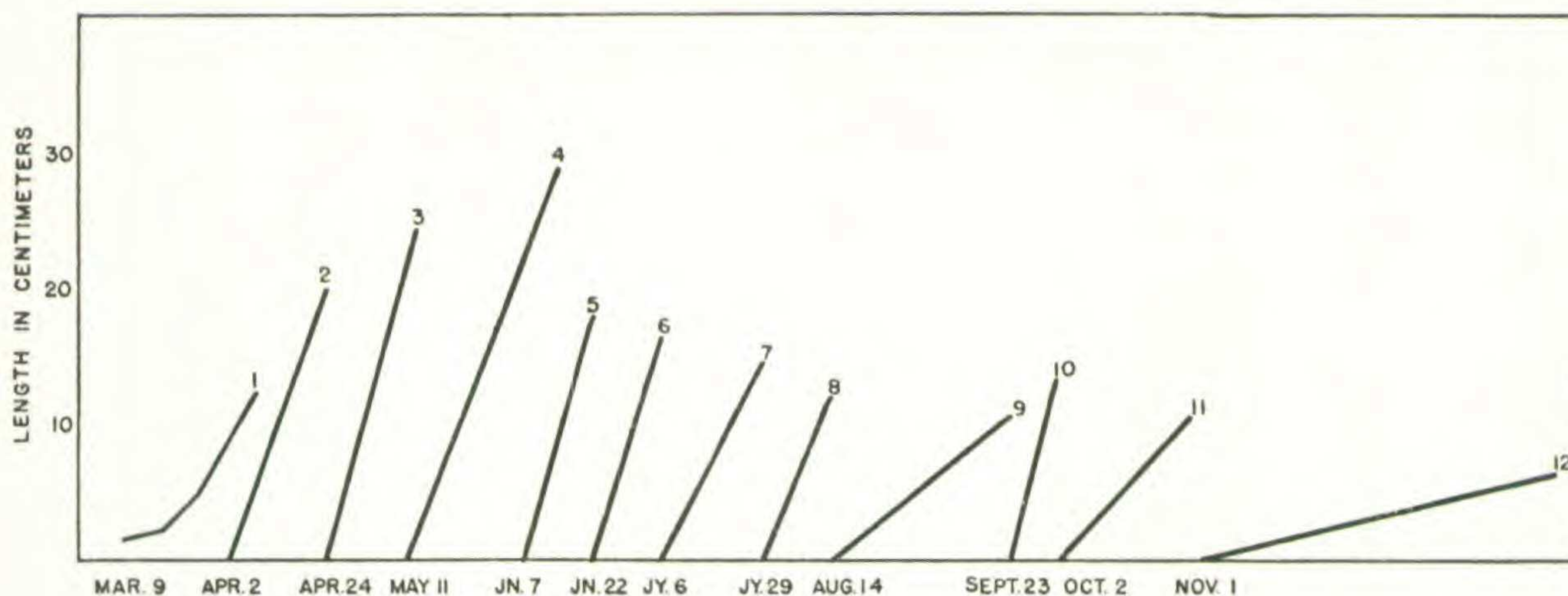


Fig. 28. Growth rates of bluegrass leaves at various times of the year. (Data for leaves 5-12 from Evans, 1949).

necessary in order to measure growth of the young leaves. This method has the advantage over measurement of individual leaves on the same plant, that curves on the entire leaf can be obtained (text-fig. 28, leaves 1-4).

Growth rates for summer and fall leaves (text-fig. 28, leaves 5-12) were drawn from data in Evans (1949). He recorded the date on which each new leaf appeared above the previous sheath on three individual plants. Each of these plants happened to produce 14 leaves during a period of one year so that an average date of appearance could be figured, and from that the interval between the appearance of successive leaves. This recorded interval was not the elongating period of a specific leaf, however, because the first observation that a leaf was growing came after it had already arisen from the growing point and extended itself up through the previous sheath *past* the ligule. About the first fifth of the growth of the blade thus takes place before its existence is recognized. The remaining $\frac{4}{5}$ then goes on to mature. Then there is a delay until the next leaf is recorded, because it has to make the $\frac{1}{5}$ of its growth up through the sheaths just as did the previous leaf. This growth begins when the previous blade matures. Not until the new leaf is exerted does the interval recorded by Evans end. His average interval between the appearance of each new leaf is therefore a composite figure, and instead of pertaining to the whole growth of one leaf it includes $\frac{4}{5}$ of the growth of one blade and $\frac{1}{5}$ of the growth of the succeeding blade. The exact proportions will vary somewhat with variation in sheath and blade length.

Evans has included the average final length of each blade in his data. If we use this information carefully we can arrive at an approximate blade growth rate for the intervals of time between leaf appearance. The recorded interval pertains to parts of two blades, $\frac{4}{5}$ of one, $\frac{1}{5}$ of the next, but the recorded lengths are for one specific leaf. If we take $\frac{4}{5}$ of the length of one leaf and $\frac{1}{5}$ of the length of the next we shall have the actual growth which occurred during a known period

of time and therefore be able to compute a growth rate. This has been done for the summer and fall leaves measured by Evans, and these rates are plotted in text-fig. 28, leaves 5–10. Since the fall leaf blades are proportionately shorter than their enclosing sheaths, the ratio of observed to hidden growth would change, and would be closer to $\frac{3}{4}$ visible and $\frac{1}{4}$ within the sheath. This correction has been applied to the last two leaves.

The following shows the way in which these rates were computed: If we assume that one leaf blade when full grown was 5 inches and the next one 3 inches and the time interval between the appearance of each one at the orifice of the sheath was 10 days, the actual growth during that time must have been $\frac{4}{5}$ of 5 inches (4 inches) plus $\frac{1}{5}$ of 3 inches (.6 inches). Total growth would be 4.6 inches in a period of 10 days, which is a rate of .46 inches per day. There will always be some error involved in such a method but the results are so compatible between leaves measured for this study and those measured by Evans that they are considered to be reasonably accurate for the present purpose. They do not agree with the data obtained in the nutrient solution experiments, where the growth rate was somewhat more than twice the natural rate at comparable temperatures. This discrepancy is probably related to the fairly high nitrogen concentration in the nutrient plus the low intensity of the light source. The complete data of text-fig. 28 do not necessarily hold for any other localities than those where the measured plants grew (Missouri and Ohio) nor to any other years than 1939 and 1949.

Periods of Rapid Growth.—Growth rate is slow in late fall, very slow in mid-winter, and sometimes rather rapid, sometimes slow in mid-summer. Most rapid growth takes place in early spring and in early fall. The spring and fall seasons have much in common for they represent a time of vigorous growth at the expense of the plant's reserves. It was first realized how definite and how similar these two periods were when rhizomes were being collected for the culture experiments described in an earlier section. Rhizomes needed in early October and March and April could never be found. They had all turned up in a flush of green growth which had involved the whole plant. At such times there is a tendency for sods to weaken and fall apart as the reserves are drawn out of old rhizomes and roots. New roots develop rapidly at these times and are short, thick, and white, in contrast to the long, thin, brownish ones of summer.

The period of rapid growth in the spring lasts from March to late April, while the fall rush is limited to a few weeks and depends to a great extent on when fall rains come. Recovery in each case is marked by the beginning of new rhizome production, but, as indicated elsewhere, the late fall rhizomes are shorter than those of summer. Though these periods have much in common, they are necessarily different, for while the carbohydrate reserves of the spring plant are greater to begin with, the progressive increase in day length and higher temperatures, together with a supply of nitrogen accumulated in the soil during cool periods, favors a prolonged period of rapid growth. During fall, on the other hand, reserves are

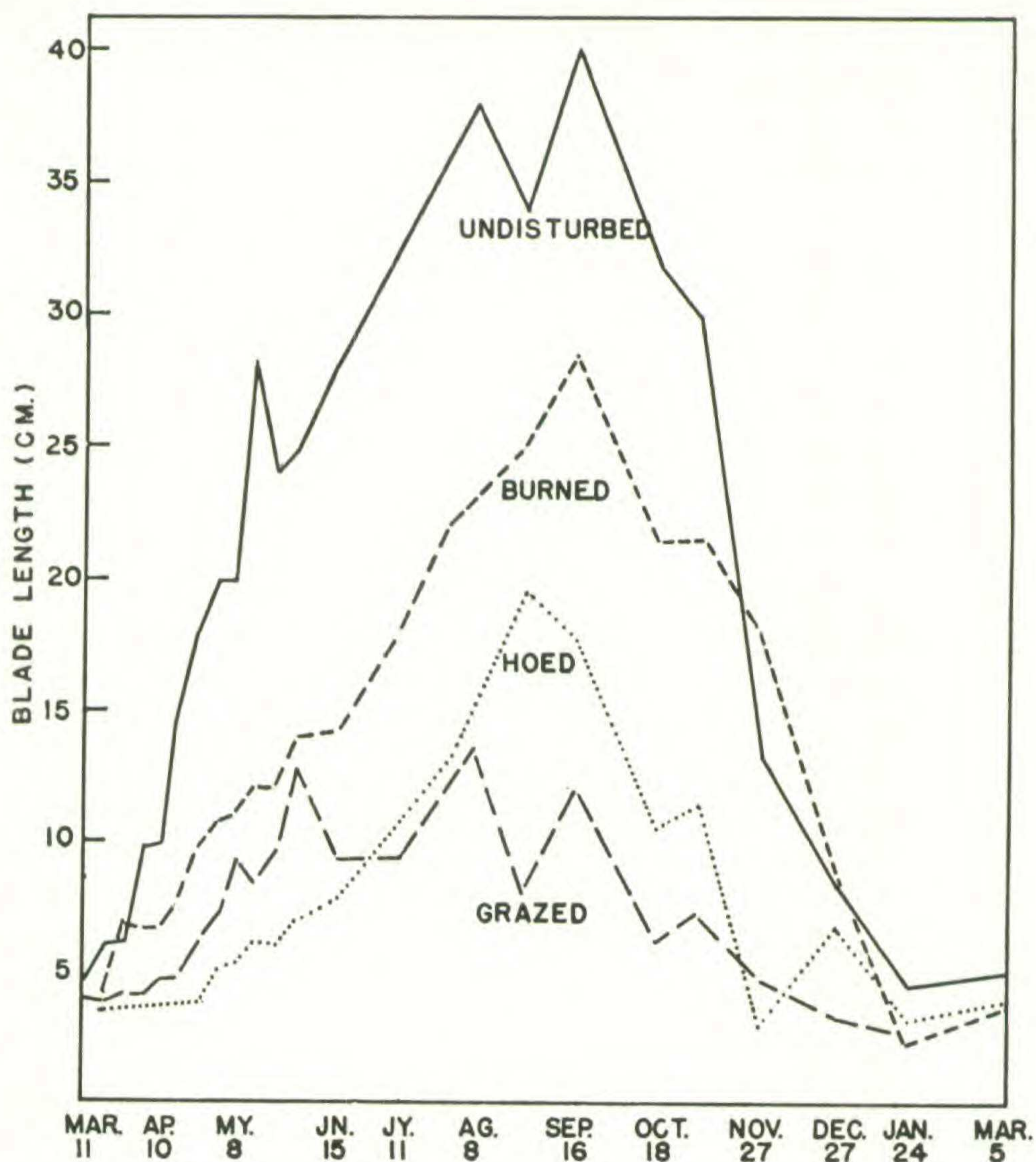


Fig. 29. Prevailing leaf-length through a period of a year under four conditions. Undisturbed grass was in an old meadow. A plot of this grass was burned in early February. Another plot was cleaned of all surface material with a sharp hoe at the same time of year. The grazed grass was in a heavily grazed barnyard area immediately adjacent to the meadow.

low following the heat of midsummer, and day length and temperatures favor a rapid accumulation of carbohydrates which is associated with slow growth. Also during summer there is apt to be considerably less accumulation of nitrogen in the soil due to bacterial fixation.

In addition to day length and temperature, there are other factors which exert considerable influence on leaf growth, either directly or indirectly. Shade increases leaf length (Watkins, 1940), though not indefinitely, since increase in length ultimately depends on amount of reserves available. Nitrogen fertilization makes leaves longer, the extent of lengthening depending on a complex of factors, among them especially time of application, type of nitrate ion (NH_4 or NO_3) and prevailing pH of the growing medium (Darrow, 1939).

Availability of water plays a part, especially in fall and winter. It has been mentioned that plants growing in soils which are prevented from freezing in winter but which are provided with adequate moisture produce very vigorous thick

rhizomes. Plants arising from these rhizomes develop remarkably fast in spring and produce exceptionally vigorous and tall plants. The relationship between fall mowing and grazing and the production of many tillers and consequent shortening of leaves has been discussed elsewhere. Denudation of soil during the period of late winter by skinning all grass from the surface of the frozen soil has been found to have a very strong effect on resulting growth of grass plants. Throughout the succeeding year leaves remain short and narrow, and lack the necessary vigor to compete with weeds. Recovery of such skinned plots is very slow. A similar effect results from skinning in August.

In text-fig. 29 a complete record of bluegrass leaf lengths throughout the year in several habitats is presented. The leaf measured was the last mature one on any given date, and 10 individual leaves were measured in each habitat. A certain amount of lag existed between the actual time of leaf growth and the time when the leaf became mature enough to measure, so that the curves do not express exactly the correlation with day length and temperature that they should. They serve, however, to give comparative results and to show the pattern of effective leaf length at any time of year.

Text-figure 28 gives a rough idea of the number of leaves produced during a year, though some allowance must be made for the fact that one or two winter leaves are not included. Leaf production varied from one every 10 or 14 days in fall and spring to one every 6 to 10 weeks in late fall and winter. Leaf production varies greatly with habitat. On a group of plants from different locations examined at the end of August, 1949, the number of leaves produced above the last intravaginal shoot of the previous winter was as follows:

TABLE VIII
NUMBER OF LEAVES PRODUCED ON PLANTS FROM VARIOUS HABITATS, COUNTED FROM LAST INTRAVAGINAL SHOOT TO LAST MATURE LEAF ON AUGUST 30, 1949

Closely grazed	Old meadow	Dry sterile meadow	Dry shady hill
11	10	9	5
10	11	9	6
10	12	7	5
11	7	8	5
14	9	8	5
16	9	8	6
10	9	8	5
12	12	10	7
12	14	10	5
10	9	9	6
Av. 11.6	10.2	8.6	5.5

Watkins (1940) has indicated that nitrogen fertilization increases the rate of leaf initiation in *Bromus inermis*.

The number of leaves which are green at any one time also varies. Thus, on March 8, 1949, plants growing in a seepy place showed development of 4 or 5 green

winter leaves while on adjacent pasture areas where the ground had remained frozen and dry most of the winter hardly any shoots had more than 2 green leaves. Evans' (1949) table showing the number of green leaves per shoot from the spring of 1939, when growth began, until the spring of 1940, when an inflorescence was produced, is presented below:

TABLE IX
AVERAGE NUMBER OF GREEN LEAVES PER SHOOT IN NON-FERTILIZED PLOTS,
ON 7 SHOOTS, EACH OF WHICH HAD A TOTAL OF EITHER 17 OR 18 LEAVES

Year	Month	Average number of green leaves		
		Entirely green	Partially green	Total
1939	May 18	2.0	.6	2.6
	June 2	1.9	.7	2.6
	June 17	1.3	1.4	2.7
	July 2	1.7	1.9	3.6
	July 17	2.0	2.0	4.0
	August 1	1.9	2.6	4.5
	August 16	2.0	2.7	4.7
	September 3	1.7	2.1	3.8
	September 18	2.0	2.3	4.3
	October 1	1.6	2.3	3.9
	October 18	1.9	2.0	3.9
	November 7-14	1.7	1.9	3.6
1940	April 1-2	1.1	1.6	2.7
	April 15-16	2.1	1.6	3.7
	May 4	3.0	1.1	4.1
	May 17	2.6	1.4	4.0
	June 3	1.3	.9	2.2
	June 17	0	.3	.3

Midsummer Depression.—Shortage of water is probably partly responsible for periods of slow growth of leaves during midsummer. Brown (1943) has shown that irrigation during periods of drought or low soil moisture helped considerably to increase yields. Ahlgren (1938) stated that moisture, more than any other factor, limited forage production. While summer irrigation may maintain yields, summer growth is made at the expense of stored reserves and may reduce the competitive ability of bluegrass against weeds (Brown, 1943). Irrigation during midsummer is probably less important than during a dry fall. Brown found fall droughts to have a decided adverse effect on bluegrass yields. Irrigation during fall and early winter is not commonly practiced, but the indications are that it would encourage root growth and tillering and thus greatly aid the grass in its competition with annual weeds.

Numerous studies have shown that peak yields of forage occur twice during the year, usually in late spring and in late August or early September (Brown, 1943). Examination of series of leaves produced by various individual plants

show that usually the midsummer leaf is slightly shorter than those immediately preceding or following it (text-fig. 29). This may be connected with the period of maximum summer temperatures which commonly occur in July. Both Harrison (1934) and Darrow (1939) have shown shortness of leaf to result at temperatures ranging between 95 and 100° F.

Since irrigation did not completely eliminate a midsummer depression of yield, Brown (1939) attributed part of the reduction to supra-optimal temperatures. Whether these midsummer depressions of forage and of leaf length are interrelated cannot be said. The spring peak can easily be understood as being a combination of factors including inflorescence development, high available nitrogen, and plenty of water, but the late August peak is more difficult to explain, unless we merely assume it indicates a return of more nearly optimum conditions.

BUDS ON THE CROWN

The Number of Buds Produced.—In a given habitat individual bluegrass plants will produce new leaves at almost the same rate, and at the end of the year will all have about the same number of leaves (table VII). In a meadow this number averages about 12–14; in a very dry shady locality, 7–9; while in a well-watered pasture it may well be as high as 18. Since under ordinary growing conditions only a single leaf blade grows at once, the longer the leaf the fewer will be the number of leaves in a given season. This accounts in part for the low number of leaves in dry shady places, for there the leaves are very long and growth is slow. In grazed places, leaves are short and the soil usually well fertilized so that growth is rapid. Consequently more leaves than normal appear. Such factors as this play an important role in the ultimate appearance and behaviour of a plant.

The number of leaves reflects the number of phytomers formed during a given period and consequently the number of buds available for rhizomes and tillers. It is very uncommon to find that all the buds on a crown have matured into new shoots, for the buds of midsummer phytomers frequently remain dormant indefinitely, thus limiting branching to the fall and winter and early spring buds. This is especially true in the case of old meadow plants.

A Conservative Crown.—Instead of speaking in abstract terms, it would be well to examine some actual plants. Text-figure 30 shows a diagram of an extremely conservative three-year-old specimen from an old meadow in early November of 1948. A photograph of the basal part of a very similar plant is shown in pl. 9, fig. 30, although only a single year's growth is included. It can be seen that in both plants only the bare minimum of buds have developed into new shoots. In text-fig. 30 two generations of inflorescences are shown, one for 1948 (I 48) and one for 1947 (I 47). On the basis of these facts, it is simple enough to put together the history of this plant. It had its beginning probably as an intravaginal shoot from some plant now long since dead. That was in the fall of 1945. During the summer of 1946 no buds developed into rhizomes, but in the fall three intravaginal shoots developed from the last three buds of the year, the 14th, 15th, and

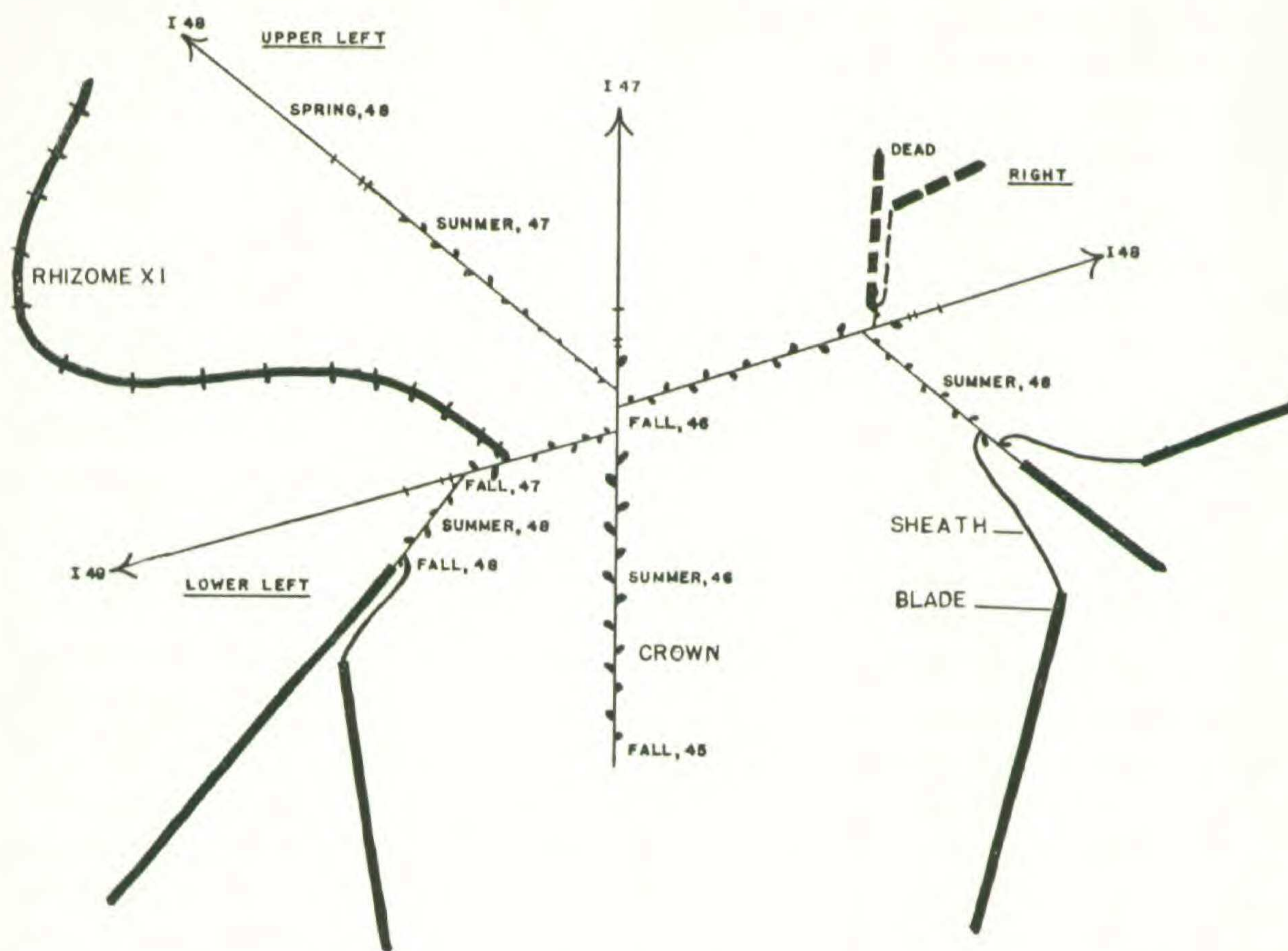


Fig. 30. Diagram of a conservative old meadow bluegrass plant. Very little branching has occurred during its three years of growth. There are few tillers, few rhizomes and most of the growing points have terminated in inflorescences. Sheath and blade, $\times \frac{1}{7}$; crown, $\times 3\frac{2}{5}$.

16th. Buds 17 and 18 which developed after the intravaginal shooting occurred should properly be considered part of the following year's growth. This main stem ended its terminal growth by developing into an inflorescence in the summer of 1947.

If we now follow the destiny of its three shoots we find that each of them pursued a somewhat similar course, at least to the extent that in 1948 they all terminated in a flowering shoot. There were, however, some interesting differences. The last shoot (text-fig. 30, upper left) did not produce any branches from its 13 buds in 1947 and thus died. The next to last shoot (right) produced 13 buds also, the last two of which developed into tillers in the fall of 1947. One of these shoots died at an early stage. In the meantime the first original shoot (lower left) produced only 10 buds of which one developed into an intravaginal shoot in the fall of 1947, and another produced a rhizome in the following summer. It will be noticed that this 1948 rhizome developed from a bud just a little below the tiller of the fall of 1947; this is the usual place of origin of most summer rhizomes when only a few develop. This rhizome is easily identified as having been produced in summer because of its length and large number of internodes.

If we follow the history of this plant into the third (1948) generation, we find that there are only three living descendants, two shoots and a rhizome. The surviving tiller on the right had produced 10 buds in 1948 up to the time it was dug up. The tiller on the left side produced only 6 buds. If we assume that only one more bud would have been added during the remainder of 1948, then the following numbers of buds were produced in each of the three years on the respective shoots:

	Upper left	Right	Lower left
Main shoot, 1946	16		
Tillers, 1947	13	13	10
Tillers, 1948	(died)	11	7

These data strongly suggest that the longer a plant lives by intravaginal shooting only, the fewer leaves are produced each year. It is also striking that over a period of three years one growing point has only increased to three new growing points, of which one is a rhizome, and two are relatively unproductive tillers.

The existence of such a conservative plant is a very precarious one. It represents the bluegrass plant at its minimum, with 1 rhizome, 4 inflorescences, and 6 intravaginal shoots being produced in a little less than three years out of a total of 74 buds.

A Vigorous Specimen.—In decided contrast to this old meadow bluegrass plant is the closely grazed pasture plant shown in text-fig. 31, which was also dug up in early November, 1948. Here the basic seasonal pattern is all but obscured. The main stem of 16 buds is much exaggerated in the drawing so that all the branching could be included. This stem developed during the year of 1947. In the fall of that year it gave rise to six branches, of which two have been broken off. Of the remaining four, the lower two, arising from buds 8 and 10, became short rhizomes, and the upper two, from buds 15 and 16, are intravaginal shoots. This main stem terminated its growth by flowering in 1948. During the spring and summer of 1948, when livestock were put on the pasture, considerable late-summer rhizome development resulted (branches A–H) and some fall rhizomes are present (I–K). The two can be distinguished because fall tillers have appeared only on the summer rhizomes; also the fall rhizomes have only one or two leaves. L and M are intermediate types. When the plant was dug up it was busy producing tillers in the axils of new fall leaves. Some branches show as many as four such tillers, and in branch F some of the tillers have already produced secondary shoots. Figure 31 (pl. 9) is a photograph of a crown region from a plant which was similar in all respects to the one shown in text-fig. 31. It bears an especially close similarity to the shoot just to the left of the 1948 inflorescence.

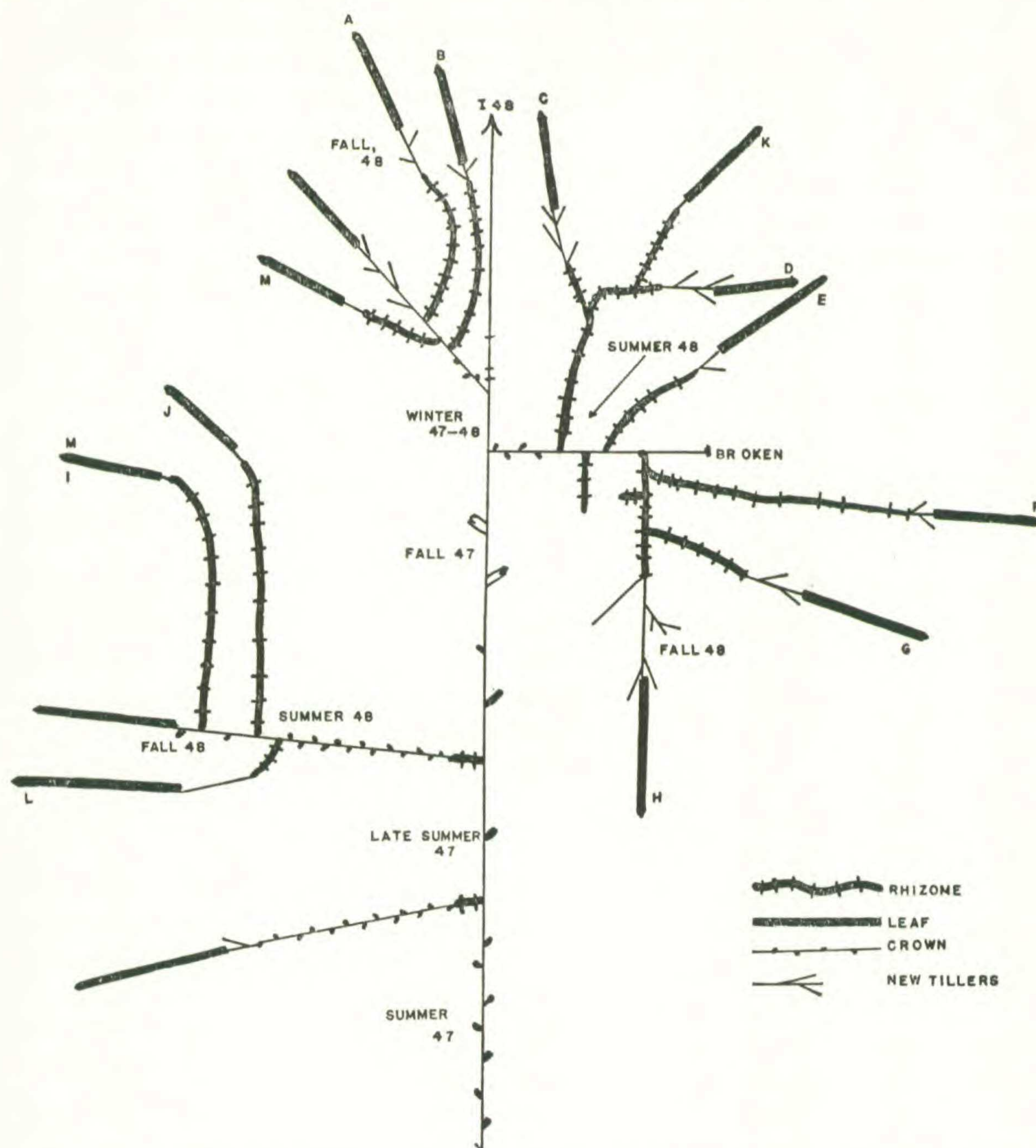


Fig. 31. Diagram of a vigorous pasture plant. Considerable development of both tillers and rhizomes has taken place during a year and a half of growth. Rhizome, $\times \frac{4}{5}$; leaf, $\times \frac{1}{4}$; crown, $\times 3\frac{1}{5}$.

To recapitulate, from a single plant in 1947, six shoots developed, two of which were broken off. Summer and fall rhizoming in 1948 increased the number of growing points by 13, and intravaginal shooting added 28 more to make a total of 45 active growing points out of a total of 138 buds. The net results of less than two years growth were: 15 rhizomes, 30 shoots and 1 inflorescence.

A Hypothetical Individual.—After examining these typical plants we may be a little closer to discerning the basic bluegrass theme together with its variations. Perhaps we can now draw a hypothetical average plant if we limit ourselves to generalities. Let us begin with a rhizome which appears at the surface of the soil

sometime in late winter or early spring as rhizomes frequently do (text-fig. 32 A-D). Such a plant will not develop any tillers. Instead, its winter and early spring buds will lie dormant while rapid leaf growth takes place. About mid-April these buds will start to swell and develop into new rhizomes. The first new rhizome will probably be short; the next ones longer; and some may grow underground for several summer months. Most of the winter and spring buds will be thus consumed in the production of rhizomes, while the late spring and early summer buds of the parent plant are gradually suppressed so that no new branching takes place. The suppression of these buds is probably related to the cessation of root initiation which Sprague (1933) has shown to take place early in May. Nishimura (1923) has indicated that no vegetative bud elongates until a root is produced. If this is true, summer dormancy is inevitable.

The sprout-like rhizomes previously mentioned as appearing in late August under rank meadow conditions would be most apt to occur on old crowns, especially on those which bloomed in spring. Rhizomes of the year, such as the one we are describing, would not commonly show them.

The change which comes over bluegrass in early fall brings with it shorter, greener leaves and white, short roots. The late summer buds, instead of remaining small, discolored and dormant, become increasingly white and well developed, but they do not usually produce rhizomes immediately. Instead, they are transitional in nature and anticipate the appearance of tillers from fall buds (pl. 9, fig. 32). Short fall rhizomes may, however, appear after several tillers have begun to function efficiently. Frequently no rhizoming at all takes place in the autumn, and the buds are thus conserved for a rapid development of rhizomes the following spring about the time the inflorescences begin to appear.

There is a conflict between rhizome and shoots for the buds of fall. Since the intravaginal shoot arises almost as soon as the bud is formed it has first choice. If conditions are right, practically all fall buds may become tillers, and thus only one or two buds will remain on the main stem from which rhizomes may appear the following spring. Where only the latest fall buds develop into tillers there is room for three or four rhizomes preceding them. If we pull these plants from the soil in late May, the former will be found to have many short leaves, and, at the most, one rhizome, and the latter will have a few long leaves and quite a few rhizomes. All rhizomes, however, do not turn up in early spring as did our hypothetical one. Some turn up throughout the summer, others in the fall. A rhizome turned up in fall is shown in text-fig. 33 A-C, for the sake of contrast. This plant begins life by tillering instead of rhizoming. Every bud at first is taken up by tillers, with the frequent exception of the lowest bud on the crown which usually remains available for production of a rhizome in the spring. In a pasture grazed closely the previous fall there are many plants of this type to be found the following spring.

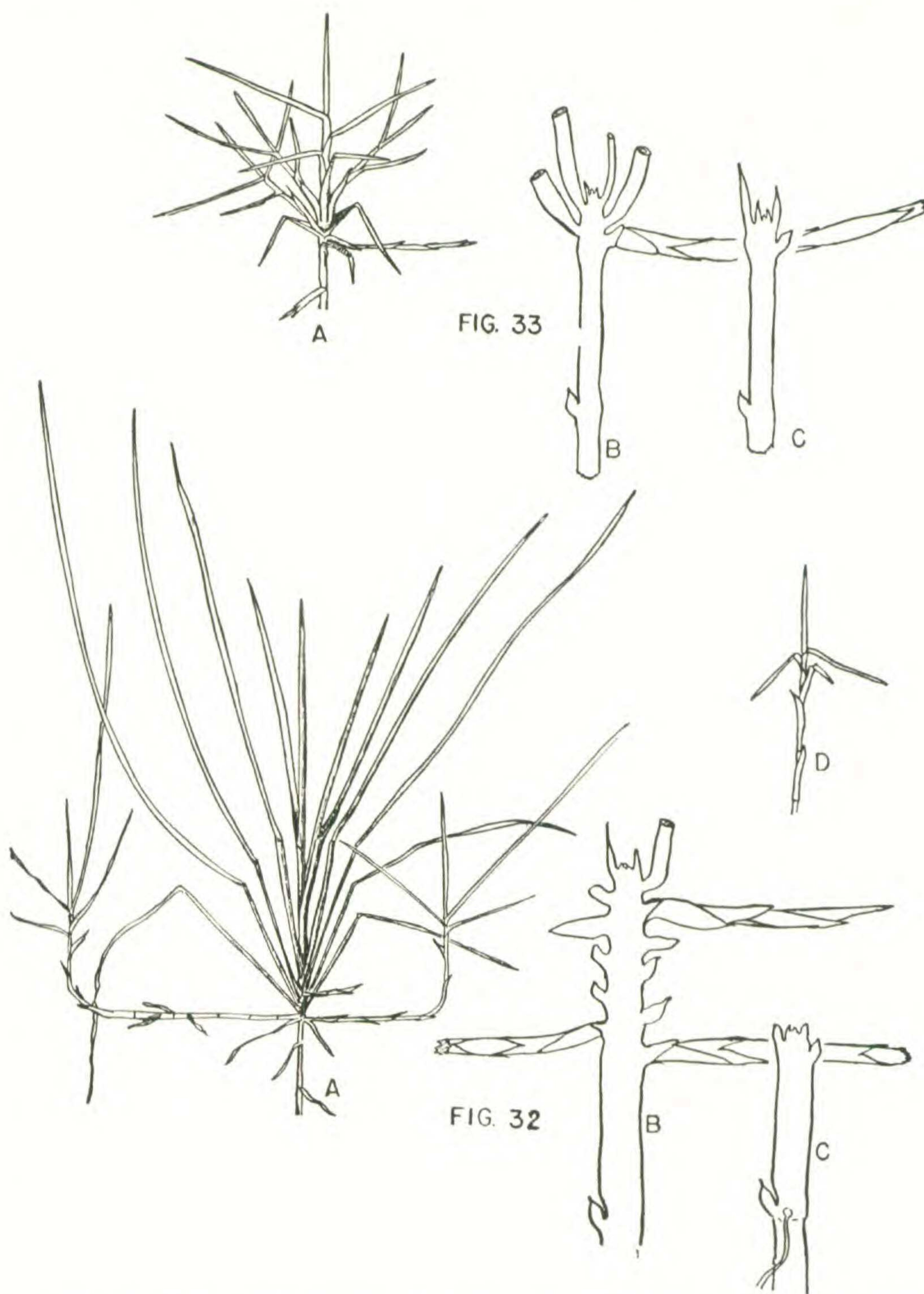


Fig. 32. A, a rhizome turning up in the spring will look like this in the fall. Summer rhizomes have turned up and formed new plants. A single short fall rhizome is developing, $\times \frac{1}{3}$. B, the crown of this same plant, showing upper buds developing into tillers, $\times 2\frac{2}{3}$. C, the crown in the spring just after having turned up, $\times 2\frac{2}{3}$. D, above, the turned-up rhizome.

Fig. 33. A, a spring plant derived from a fall rhizome, with three tillers and short winter leaves, $\times \frac{1}{3}$. B, the crown in spring, with only a single rhizome at the base, the remaining buds occupied by tillers, $\times 2$. C, the crown in fall shortly after having turned up, $\times 2$.

Some Practical Considerations.—While the seasonal effect is more or less the same, the record of events as recorded by various generations of rhizomes will be slightly different. The proportion of rhizomes of a given vintage in a sod or a nursery plot may change considerably depending on the age of the stand, the treatment it receives, or on the weather. Evans and Ely (1935) have presented figures which show the extent of such variation within two successive years:

TABLE X
AVERAGE NUMBER OF NEW RHIZOMES PER PLANT IN DIFFERENT MONTHS IN 1932 AND 1933 ON PLANTS TRANSPLANTED ON MAY 18, 1931, TO CULTIVATED ROW PLATS. (THE PLANTS WERE NOT CLIPPED AT ALL.)

Month	1932	1933
April		0.0
May		0.3
June	15.5	5.3
July	18.3	2.0
August	3.3	21.0
September	0.3	6.0
October	2.3	0.5
November	3.0	

Wherever studies of bluegrass are made, the sequence of events and their possible variation must be kept in mind. Undoubtedly, elaborate quantitative tests of rhizome production, top production, or other aspects of the plants' growth have failed to obtain consistent or statistically significant results because of the failure to reckon with the flexible nature of the species. In pot experiments with nutrient solution it is doubly important to know the kind of material being grown in the pots. Such factors as the number of buds available on a transplanted rhizome or crown, the time of year such buds developed, the length of the associated leaf, and whether the rhizome is from a turf or a nursery row will all have repercussions on the results.

DESIGNING A BLUEGRASS PLANT
THE SPECIFICATIONS

How we manage bluegrass will depend on how we intend to use it. Bluegrass is called upon to serve many purposes, including the following:

<i>Pasture</i>	<i>Range</i>	<i>Meadow</i>	<i>Conservation</i>	<i>Turf</i>
Alternating	Winter	Hay	Sod run-off strips	Lawns
Continuous	Summer	Silage	Terrace plantings	Greens
Dairy	Breeding		Roadsides	Fairways
Fattening				Playing fields
Subsistence				Landing fields

With adequate study of each environment and of the factors involved in each type of use, a blueprint could be drawn showing the specifications of the plant needed. There would always be some conflicts. It might be a simple matter to

design a plant for yield in one year, but consideration would have to be given the repercussions of management techniques on future production. There is a strong likelihood that the most efficient treatment of a bluegrass stand might involve making different use of it in successive years. Under some conditions this is not feasible so a compromise must be made.

THE MATERIALS AND THE LABOR

We have found that the bluegrass plant is a flexible collection of buds whose destiny, while in part controlled by inaccessible aspects of its environment, can also be molded by specific practices. Once the requirements are known, we can choose from the following alternatives:

1. *Many vs. Few Buds*.—The highest production of buds comes with short leaves, moist, nitrogen-rich soil, and sunny conditions. Where intensive management is necessary, usually the more buds the better. If long leaves are desirable then some sacrifice of buds is inevitable.

2. *Dormant vs. Sprouted Buds*.—Greatest sprouting of buds occurs in good soil with plenty of aeration and little competition, and seems to be aided by high organic-matter content and adequate water supply. (It is just such requirements which Percival (1921) specifies as necessary for maximum development of tillers in the wheat plant.) It is generally desirable to have a large proportion of the buds on a plant develop. This can be carried to extremes, however, as discussed in the next section. If the need is for a tight sod, then competition among individuals will necessarily follow, and some loss of sprouting ability will be encountered.

3. *Rhizomes vs. Tillers*.—Tiller production is encouraged by provision of good soil conditions as described above. Treatments which specifically favor tillers include fall grazing or mowing, fall nitrogen fertilization, removal of all shading growth and dead weeds, and in dry falls the addition of moisture. Maximum tillering may not always be desirable. It can result in what one might call an excessive investment in growing points, considering the amount of capital (soil, oxygen, water, and nutrients) which the plant has within reach. Ideal conditions are necessary to support large numbers of closely packed shoots even though they are capable of forming their own adventitious roots. When such plants are subjected to excessive mowing or grazing or treading their reserves can be very rapidly depleted. This is especially true since strongly tillering plants seldom have very extensive underground parts. In general, it should be stressed that if shooting is to be encouraged in fall, then adequate provision should be made to provide optimum conditions for growth in the following spring, especially through nitrogen and potassium fertilization.

Rhizome development depends in part on how extensive the fall tillering process has been. If most of the fall and winter buds have been used up, rhizomes are apt to be uncommon. The same ideal soil conditions which encourage sprouting of other buds favor the production of rhizomes. Plants which grow in open soil

as spaced seedlings or shoots in nursery plots are abnormally productive. Balanced fertilization in winter, spring, or summer favors increased rhizoming. Phillippe (1943) found that in nutrient culture, maximum rhizome production occurred under conditions of moderate nitrogen concentration (17 to 57 PPM) and by fairly high potassium concentrations (41 to 162 PPM). High nitrogen content has been found by numerous investigators to reduce rhizome production in pot and nutrient experiments. Brown (1943) has stated that summer irrigation leads to the death of many summer rhizomes, and Harrison (1934) found combinations of close clipping and temperatures around 100° F. to be fatal. This coincides with observations of Wilkins (1935) that over-grazing during drought periods when temperatures were around 100° F. reduced bluegrass recovery the following fall by 75–99 per cent.

To some extent rhizome production is self-regulatory. Usually whenever high production is a possibility, as in new seedlings or broken sods, some benefit may be derived from much rhizome growth. When sods are tight, then fewer buds sprout. Under an old sod, rhizome production apparently reaches an approximate equilibrium with the available soil nutrients, especially nitrogen. There is adequate decomposition of a certain amount of dead rhizome matter plus just sufficiently vigorous growth of the plant itself, so that no more rhizomes will be added to the soil that can be broken down the following year. Some fluctuations in this cycle will occur with weather variations.

A certain amount of rhizome production is essential under most conditions because intravaginal shoots seldom persist for more than a year. It is also important, in view of the many advantages of rhizome herbage production, such as the broader, more vigorous leaves, more even distribution of roots, growing point well below the soil, shorter sheaths, and leaves close to the soil, that plants are not completely defoliated by grazing. There is little doubt, however, that too high a proportion of rhizomes in the stand may lead to low herbage productivity, for they respire and consume soil oxygen, and sooner or later die, and the micro-organisms which break them down compete with the grass itself for soil nutrients. This is especially true since rhizomes are high in carbohydrates and low in nitrogen.

It is commonly found that where fields or plats are mowed during the summer for a period of years, total forage production falls off. Ahlgren (1938) states: "The data show that with the exception of 1933 (the second year) there was a progressive and significant decrease in the yield of bluegrass on all plats, regardless of the cutting or fertilizer treatment used during the period 1932-1936 inclusive." His data follow:

Year	4-inch cut		Hay cut	
	No fertilizer	Fertilizer	No fertilizer	Fertilizer
1932	1,619	3,113	2,050	3,957
1933	2,153	4,295	2,977	4,579
1934	1,817	2,114	1,681	2,046
1935	1,520	1,932	1,279	1,785
1936	826	1,703	435	1,617

(This test was begun on old sod. The first cuts were made as above, to a level of 1½". Subsequent cuts were made to 1½" level when the grass reached a height of 4-5". Figures are pounds per acre.)

The cause of this progressive decrease in production has not been adequately explained, but there is a strong possibility that the accumulation of rhizomes in the soil may be involved. That such accumulations occur are well shown by data from Brown (1943):

Year	Herbage yields			Root Yields			Rhizome Yields		
	1"	2½"	Hay	1"	2½"	Hay	1"	2½"	Hay
1937	2833	2254	5857	1927	2049	1922	122	122	108
1938	508	310	1280	1897	2137	2210	372	478	505
1939	382	141	501	1979	2289	2281	398	519	507
1940†	1286	900	1601	1946	2088	2455	660	817	1071

†NaNO₃ added 100 lbs. per acre March 15 and semi-monthly at rate of 50 lbs. per acre from April to June 15 and from Aug. 15 to Sept. 30. These test plots were seeded in Sept., 1936. Figures are lbs./acre. 1½- and 2½-inch cuts were made semi-monthly. Hay cuts made at full bloom and at end of growing season.

The same progressive decrease in yields of herbage are apparent here. In both of these experiments, the removal of clippings from the plats probably exerted some influence on total yields. It is clear, however, that reduction in yield paralleled an accumulation of rhizomes. Brown has stated that death of rhizomes began in the second year, and in the fall of the third year there were so many dead ones that they were separated from the live ones and not included in the data. Therefore the figures above do not show the total accumulation of rhizome material in the soil. The data would have been even more striking had all dead material been included.

Typically, maximum herbage yields were secured the first year after seeding. In that year the rhizome dry matter in the soil was less than 5 per cent of the total dry weight of the herbage and rhizomes together. By the third year herbage yields had dropped from eight to sixteen times, but rhizome weight had increased from three to five times. Rhizomes had come to make up 50 per cent or more of the total

dry weight exclusive of roots (which had a remarkably constant dry weight throughout the tests). Significantly, the least amount of rhizome dry weight was produced when the grass was mowed semi-monthly to a 1-inch level. Most of this difference probably involved rhizome length rather than number.

In the fourth year heavy nitrogen fertilization in spring and summer increased herbage yields from three to six times but at the same time the rhizome dry matter was nearly doubled. Addition of nitrogen in both Ahlgren's and Brown's tests increased yields but did not completely restore productivity to its former level. According to the data above, rhizome production was greatly increased by fertilization in spring and summer, and the sod-bound condition could be expected to become worse the following year.

Moderate mowing of pastures in early spring through summer apparently will increase the rhizomes in the soil in proportion to the amount of tops above ground, even when mowing may be semi-weekly to a height of 1 inch. Increase of rhizomes goes on until the stand is almost devoid of herbage value. Rhizomes do eventually turn up and add to the herbage total, but there is considerable delay and wasted energy in getting top production through rhizomatous plants alone. Not only that, but at the most an ordinary plant cannot be expected to bear more than four or five rhizomes while its potential of new tillers is considerably greater when properly managed.

The 2½-inch height such as that advised for most lawn mowing resulted, in Brown's experiments, in the highest proportion of rhizomes to tops. This would give a tough sod, but relatively little top growth, unless some counteracting practice designed to stimulate intravaginal shooting and long leaf growth were used.

Kentucky bluegrass is really a plant with a split personality. It is trying to be rhizomatous, as is its relative, Canada bluegrass, and upright, as is *Poa trivialis*. It actually can assume either role, and it is up to the pasture or turf manager to decide which personality or complex he prefers.

It is not surprising that to some extent bluegrass has lost some ground in the field of intensive pasturing to non-rhizomatous grasses and legumes, for these species do not waste energy and nitrogen on non-leafy production. Admittedly, bluegrass cannot compete with such productive non-rhizomatous types as alfalfa, perennial ryegrass, orchard grass, and ladino clover, but its quick adaptability and persistent nature are indispensable attributes under many conditions. To make maximum use of the species, however, close attention must be paid to its seasonal rhythm and its system of bud economy.

4. *Long vs. Short Rhizomes.*—Summer rhizomes are long, and fall rhizomes are short, but close and continuous grazing leads to short rhizomes at any time. In pot cultures Harrison (1934) found that high nitrogen content encourages short rhizomes. Length of internode has little or no relation to ultimate length of the rhizome. Dry periods shorten internodes but variation in nutrient balances has been shown by Phillippe (1943) to have no significant effect.

Short rhizomes are desirable in some cases, long ones in others. If a tight sod is required, rhizomes of moderate length must be encouraged. Stands which have only short and shallow rhizomes will have little protection under very hot and dry conditions. If properly managed, however, short as opposed to long rhizomes could be counted on to increase the efficiency of a pasture or lawn.

5. *Branched vs. Unbranched Rhizomes*.—Branching of rhizomes is encouraged by those conditions which favor the development and sprouting of buds. Damage to the initial growing point stimulates axillary buds to develop, and wherever summer sods are burned or mistreated, or submerged by dense weed growth or by alluvium, the ability of rhizomes to sprout in early fall from their axillary buds is of great importance to the survival of the plant. The vigor of the rhizome determines how many buds develop, and whether they will form strong rhizome-like branches or merely delicate vertical shoots. For those strains of grass which are primarily rhizomatous, thickness of the stand is almost completely dependent on the ability of the rhizome to produce branches.

6. *Vegetative vs. Reproductive Shoots*.—The number of reproductive shoots produced in May depends on two things, the number of plants which are adequately mature and vigorous enough to undergo flower initiation in the previous fall, and the number of tillers which these plants produce. Plants which are mature and vigorous in fall will have come largely from rhizomes turned up during the previous fall, spring, and early summer. Some perennial tillers will contribute to the cause. Ultimately then, to influence the potential seed crop it is necessary to start work a year and a half ahead of harvest time. Encouragement of rhizomes, followed by encouragement of tillering, followed by encouragement of long leaves and full panicles as described below, should give maximum seed yields. This would leave the soil full of old rhizomes, and unless steps were promptly taken to deplete their reserve carbohydrates through grazing and encouragement of tillering the following fall, subsequent yields would suffer. A complete management plan would be more complex than this, but these are the main considerations. Such a plan might also provide high yields of hay or silage, but maximum development of inflorescence may not always be desirable. Limitation of flowering can be accomplished through heavy grazing in late summer and fall, and by grazing or mowing in spring when the panicles are exerting. Encouragement of a vegetative condition in bluegrass holds back the spring flush of growth which accompanies the development of the flowering shoot. It also holds the protein content of the grass at a fairly high level, while the carbohydrates are kept low (Woodman et al., 1928; Hein, 1937). This would limit the gaining of weight by fattening animals in preparation for fall markets or over-wintering. It would, on the other hand, encourage summer milk production in a dairy or breeding herd.

7. *Short and Wide vs. Long and Narrow Leaves*.—Short, wide leaves and excessive tillering often go together. Long leaves are encouraged by winter and spring fertilization. When heavily tillered plants are fertilized in winter and spring a very

dense, moderately long and wide-leaved blue-green plant is produced which is highly productive. It combines the advantages of the other types.

Constant grazing or mowing keeps grass leaves short, probably for two main reasons. First, without the over-burden of shading tops, the blades reach the light rapidly and do not become attenuated. Second, such treatment encourages the production of many short rhizomes the early leaves of which are commonly somewhat abbreviated. Infrequent mowing or grazing has little effect on leaf length. While long-leaved plants are commonly considered more productive of herbage, the fact remains that short, wide-leaved foliage is more palatable to livestock. They will barely consider the rank growth of mid-summer meadows.

8. *Heavy Seed Production vs. Little Seed.*—There is a complex relationship between number of panicles and number of seed produced. In general, number of panicles is increased by mowing or high nitrogen fertilization in fall (Spencer et al., 1949; Nillson-Leissner, 1937). This treatment, however, usually reduces the panicle length and the culm length and reduces the number of seed set per panicle when compared to spring fertilization (Phillippe, 1943; Spencer et al., 1949; Nillson-Leissner, 1937). Winter or very early spring fertilization tends to give tall panicles and inflorescences, but does not increase the number significantly. Seed production is generally good. Late spring applications in April, when the panicle is growing, tends to encourage leaf growth rather than inflorescence development, and results in a weakening of the culm and reduction in quality of the seed.

9. *Sod vs. Open Growth.*—Bluegrass, like most other plants, grows most profusely when grown alone. When it is allowed to sod over, then we inevitably lose production, whether it be of forage or seed. In this respect it is significant that bluegrass plants growing in alluvium produce by far the greatest amount of seed per panicle, bear a goodly number of panicles, have large seeds, and long and wide leaves. A year-round supply of water, rich soil, and sun combine to produce maximum yields. Inevitably in a sod we have to sacrifice some greenness, some vigor, some thickness of stand. From a productivity standpoint the best that can be done is to provide management practices which make the sod-grass think it is down by the river. Discing and harrowing aid in this simulation by providing loosened and bare soil areas. To avoid weediness treatment should be done only in fairly late fall when tillering, rooting, and fall rhizoming together can recover the vacant areas while weed growth is at a minimum. Another way of getting the productivity of the river bottom up on the pasture is by using alluvial ecotypes for seed. This process is going on more or less unconsciously in many grass-breeding experiments. So-called high-producing strains of many species invariably bear a striking resemblance to river-bottom types.

THE PARTS OF THE BLUEGRASS PLANT COMPARED⁵

WHERE DO THEY ORIGINATE?

Rhizome.—From underground, axillary, mature buds whose subtending leaves are dead, or dying. April–May extension type predominantly from buds of early fall and early spring. August sprout type from spring and summer buds, and fall rhizomes from early fall buds.

Crown.—From underground terminal buds of rhizomes, seedlings, or intravaginal shoots. May sometimes be above ground, especially in seedlings and shaded shoots.

Tiller.—From axillary buds below or above ground on late fall and early winter phytomers.

Culm.—From terminal bud of crowns of sufficient maturity. If from a rhizome, the crown will not have less than 6–8 leaves; if a tiller may have only 2.

Panicle.—Main axis or rachis is continuation of culm. Side branches arise as secondary, tertiary, and quaternary protuberances from this rachis.

Spikelet.—Some time in April.

WHEN DO THEY BEGIN TO FORM?

Rhizome.—Principally early May, concomitant with flowering, but to some extent throughout early summer; also in fall, early or late, depending on condition of grass. Sprout type in late August or early September on rank meadow type or burned or damaged areas. In closely grazed places on good soil almost all year except late winter.

Crown.—When rhizome turns up, especially late summer and early fall, and late fall and early spring. From tillers in late fall and winter and from seedlings in fall and spring.

Tiller.—Early fall to late winter, principally late fall.

Culm.—Internodes develop in late fall and winter following initiation of intravaginal shoots.

Panicle.—Winter and early spring; may not form until early March (Musgrave, 1940).

Spikelet.—Some time in April.

NUMBER ON A PLANT OF 16 PHYTOMERS PER YEAR

Rhizome.—Varies greatly, 0–8, average probably 2, but including secondary and tertiary plants may be 4–6.

Crown.—Main crown, plus average number of turned-up rhizomes (2) plus average number of tillers (3, see below) gives average of 6; may be greatly amplified by secondary and tertiary budding.

Tiller.—Average around 3, less than 1 or more than 10 infrequent; with secondary branching may reach 50.

Culm.—Usually 1 on main axis and 1 on each of 1 or 2 tillers. May be up to 12 per plant with multiple tillering.

Panicle.—One per culm; number of protuberances may vary greatly; average 3–5 at each node of rachis. There are from 5–10 rachis nodes, therefore 15–40 branches on main axis. Secondary and tertiary tillers have fewer.

Spikelet.—Average number not counted. Secondary and tertiary tillers have fewer.

TO WHAT EXTENT DO THE PARTS BRANCH?

Rhizome.—Usually limited; can be extensive.

Crown.—Branching includes rhizomes or tillers. Of 16 buds, not more than half usually develop.

Tiller.—Branches as does crown; may form rhizomes or secondary tillers, but only the latter in first fall and winter. Rhizomes rarely appear until following May, from any left-over buds.

Culm.—Does not branch (no buds present).

Panicle.—Almost all buds develop.

Spikelet.—Basal phytomers including the two glumes and lowest lemma do not usually bear branches. Upper phytomers bear florets.

⁵These data are a composite of information from authors previously credited, and from observations made in the course of the present study. They are in most cases very approximate, and variation could not always be taken into consideration due to lack of data. Most of the data pertain to bluegrass growing in Missouri.

THE LENGTH OF THE INTERNODES

Rhizome.—Highly variable in length, 1–50 mm., average 10–15. Shorter in dry soils or dry periods.

Crown.—Minute, somewhat less than 1 mm.; individual internodes can be induced to elongate by shading or covering plant with soil.

Tiller.—Same as for crown.

Culm.—Gradational, the first a few mm., the last up to 30 cm. or more. Successive internodes plotted on a logarithmic scale fall on a straight line, under normal conditions. (See Prat, 1934.)

Panicle.—Gradational on rachis, in reverse order to internodes of culm. Range from 30 to 2 mm., but do not form a straight line on either natural or logarithmic scale.

Spikelet.—Longest below first glume, 1–3 mm.; rest are minute.

THE NUMBER OF INTERNODES

Rhizome.—Many in summer extensor rhizomes—may be up to 30. Fall rhizomes seldom show as many as 10, usually 5 or 6.

Crown.—Depends on habitat and season. From 7 to 18 a year.

Tiller.—Same as for crown, but few tillers persist for a whole year. If they do, there tend to be fewer phytomers each year.

Culm.—3–5, usually 4, rarely 6.

Panicle.—Rachis 5–10, main branches about the same, branches of lower order successively fewer.

Spikelet.—Averages 6, varies from 4–10 (includes 3 sterile and 3 or more fertile).

HOW FAST DO ITS INTERNODES ELONGATE?

Rhizome.—2–5 mm. per day.

Crown.—No elongation.

Tiller.—No elongation.

Culm.—Varies with the internode number. Internode 1, 0.5 mm. per day; Internode 2 and 3, 4 mm. per day; Internode 4, 7.5 mm. per day.

Panicle.—7 mm. per day for rachis as a whole.

Spikelet.—Very little if any elongation.

THE SHAPE OF THE INTERNODE; IS IT SOLID OR HOLLOW?

Rhizome.—Compressed dorsoventrally, solid.

Crown.—Round, solid.

Tiller.—Round, solid.

Culm.—Round, hollow.

Panicle.—Round, somewhat ribbed and grooved at extremities; hollow, solid at extremities.

Spikelet.—Not examined.

WHAT KIND OF LEAVES, IF ANY, DOES IT BEAR?

Rhizome.—Cataphylls only; very short blades may appear (up to 2 or 3 mm.) without turning up.

Crown.—First leaves with fairly short blade, shorter than sheath; later, blade is longer.

Tiller.—Leaves as for crown, but first leaf is enclosed in prophyll.

Culm.—Normal leaf at base, upper leaf has very short blade and long sheath. Others transitional. No leaf on last internode.

Panicle.—No leaves.

Spikelet.—Presumably glumes are sheath part of leaf; palea is prophyll of the shoot which becomes the floret.

WHAT POSITION DOES EACH PART ASSUME?

Rhizome.—Horizontal, inverted arch, almost upright, or may show some geotropism at first.

Crown.—Horizontal to vertical.

Tiller.—Nearly prostrate to erect.

Culm.—Usually vertical, though under special conditions may be prostrate or procumbent.

Panicle.—Attitude of rachis same as culm. Branches may be appressed to drooping, though usually at right angles.

Spikelet.—Florets usually fairly closely appressed.

WHAT IS THE NORMAL LIFE OF EACH PART?

Rhizome.—May turn up within a few days after it begins to grow, or may stay underground 60 days or more in summer. During cold weather remains underground while soil is frozen.

Crown.—Matures with development of flowering shoot; shortest period is on fall intravaginal shoots, only 6–7 months. Rhizomes which turn up in late summer may bloom in 9 or 10 months, and intravaginal shoots which do not bloom first year may bloom in 1 year and 6 months. Fall seedlings take 1 year and 8 months and spring seedlings 1 year and 3 months.

Tiller.—6 months, or 1 year and 6 months.

Culm.—Initiation of the phytomers involved takes only a short time in late fall; elongation in spring takes about 1 month. Total life is about 6 months.

Panicle.—5 months for elaboration of branching system, 9 or 10 days for elongation of the panicle proper, and 45 days for its complete exertion including culm elongation.

Spikelet.—First spikelet starts to form when panicle is about $\frac{1}{4}$ inch long. At 1 inch there are at least 3 rudimentary florets. Glumes enclose entire spikelet at $1\frac{1}{2}$ inches (Musgrave, 1940). This would be 5–7 days. Total maturity time, to exertion of anthers, about 5–6 weeks.

HOW FAST ARE NEW PHYTOMERS INITIATED?

Rhizome.—Rapidly, averaging nearly one every two days during summer.

Crown.—Average around 13–14 a year, exclusive of inflorescence. Slow in winter and hot or dry periods of summer; rapid in spring and for a brief period in early fall. A new leaf every 15–20 days in spring and early fall; every 30 to 50 days in summer and late fall; and every 60 days or more in winter.

Tiller.—Same as for crown.

Culm.—4 phytomers of the culm produced some time in late fall but rate not known.

Panicle.—Assuming 8 internodes on each rachis in period January 1 to April 1, rate is about 1 phytomer every 11 days. Comparable rate on vegetative part is 1 about every 60 days. Rate of branching is different, depending on strain and time of year; averages about one new generation every 40 days according to data in Evans (1949).

Spikelet.—A spikelet with 3 rudimentary florets develops in about 6 days (Musgrave, 1940); including glumes this is about 1 phytomer per day.

THE FREEDOM OF THE PHYTOMER

A grass plant is a community of phytomers. No phytomer exists autonomously, but is necessarily involved in the total effort of the plant. At the same time, in its extreme youth an individual phytomer is quite plastic and may, as it ages, develop into any one of a number of things. It may or may not take full advantage of its potentialities to produce leaf blade and sheath, internode, root, and bud. It may consist only of an internode, as in the case of the last phytomer of the culm. It may be only an internode with a branch as in the panicle. It may be an internode and a sheath and blade, as in the lower culm internodes, or an internode, sheath, bud, and root, as in the rhizome. Sometimes, there is no well developed internode, and only the sheath, blade, bud, and root are prominent. Rarely, an internode, sheath, blade, root, and bud are all present as in stoloniferous shoots. We can summarize the various main combinations of the five structural elements on phytomers of various parts of the plant as follows:

Phytomer location	Internode	Sheath	Blade	Bud	Root
4th culm	Long	0	0	0	0
Lower culm	Medium	Medium-long	Medium	0	0
Panicle	Medium	0	0	Usual	0
Spikelet	Minute	Short	0	No floret	0
Crown	Minute	Medium	Short to long	Usual	Usual
Rhizome	Medium	Medium	0 to minute	Usual	Usual

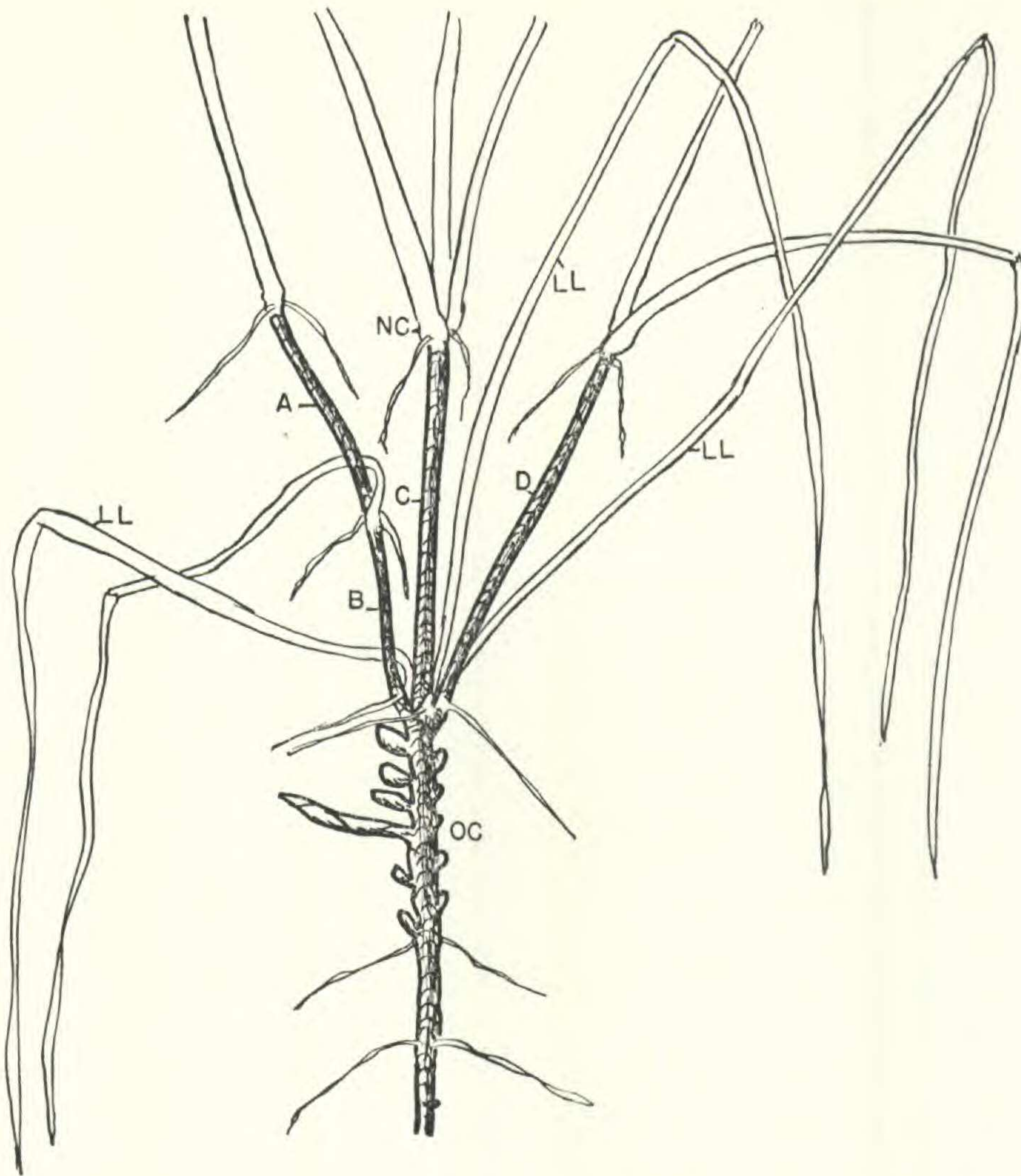


Fig. 34. In fall and spring when vegetative shoots are covered over by alluvium or manure, or by soil excavated by gophers, the internodes on the phytomers which are just maturing will develop long internodes such as A, B, C, and D, even though the leaf blades of the phytomers (LL) are long; OC, the old crown, now buried; NC, the new crown.

Intermediate combinations of the above structures may occur under special circumstances or in areas transitional between different parts of the plant. A distinctly different ratio exists between the three prominent features of phytomers (blades, sheaths, and internodes) when they are located on a rhizome, flowering shoot, and vegetative crown. Under certain circumstances these ratios can be altered by subjecting the plant to changed external conditions. If the plant is shaded, internodes will elongate in spite of the presence of leaves. This occurs in vegetative shoots which are shaded by heavy mown grass or covered by soil, as often happens around gopher mounds (text-fig. 34). Where such growth follows mowing, the growing point is raised out of the ground with the result that it is easily killed by drought, cold, or trampling.

A somewhat similar departure from normal behaviour can be noticed on rhizomes grown under special conditions. We have discussed the fact that rhizomes turn up when leaves begin to develop. If the rhizome is enclosed in a glass tube

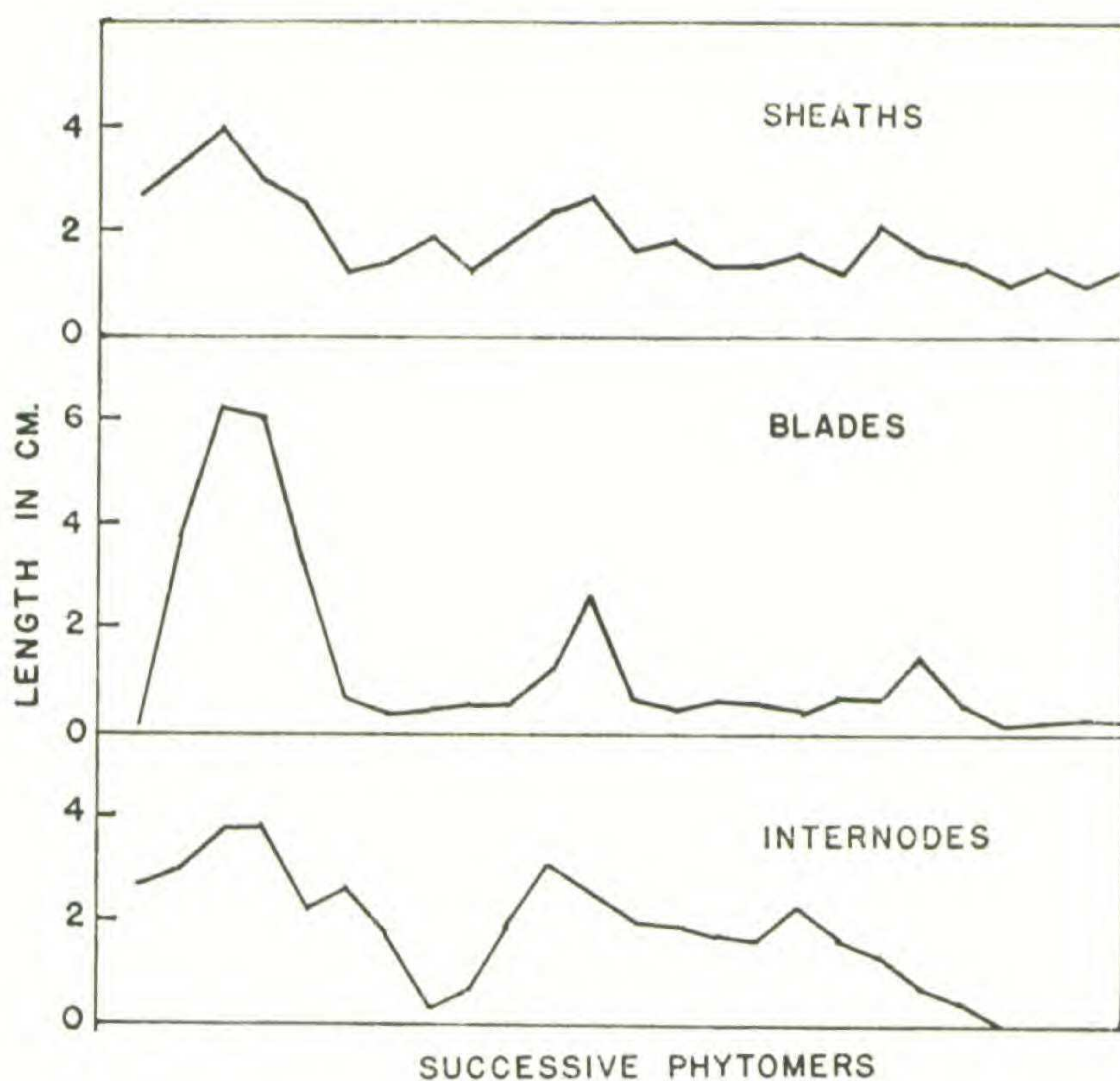


Fig. 35. A rhizome was prevented from turning up by directing it into a glass tube buried in vermiculite. The rhizome grew for several months, and was then removed and its phytomer parts measured. These measurements are shown above in the form of curves of growth.

and its leaves prevented from reaching the light, as was done in an experiment (see pl. 2), the sheaths and internodes become abnormally long. Such a rhizome is illustrated in text-fig. 35. From this diagram it can be seen that the response of the blade, sheath, and internode to the stimuli coming from the parent plant are different. While the internodes tend to respond with considerable sensitivity to prevailing conditions, the leaf blades increase in length only when the stimulus passes a certain threshold. Sheaths as usual appear to be somewhat intermediate in their reaction, embodying features of the two other organs.

The physiological basis of this manner of growth was not investigated, but the data indicate, in part, how correlations between plant parts can appear to exist at particular times and at other times to have no apparent basis in fact. It also shows that a process which normally seems irreversible can be reversed upon occasion. The trend from rhizome to shoot is commonly observed. The reverse trend is seldom witnessed or imagined possible. The reversal of differentiation in more advanced parts of the plant, as in the development of so-called viviparous shoots in the spikelet or in the appearance of leaves on the panicle, has been discussed by Sharman (1947). The mere appearance of glumes and lemmas after all leaf forms had been suppressed is also a form of reversal.

The development of any given phytomer apparently is a complicated matter which involves a great many variables operating on the plant through its physio-

logical systems. While phytomers are plastic and can be affected by environmental factors, they nevertheless eventually resolve themselves into a consistent pattern which becomes the mature plant of the proper species. This argues for some sort of internal control. Such control, however, must be of a secondary nature, since the achievement of such features of the mature plant as the inflorescence ultimately depend on environmental factors. Thus while the development of a panicle on a growing point undoubtedly affects the internode beneath it, the panicle would never have developed at all had it not been for the fact that the plant had been exposed to a certain combination of environmental conditions. Also the panicle's effect will depend on conditions of the moment and the habitat. There are thus primary environmental influences and secondary internal situations which affect the fate of a given phytomer, but they do not operate independently. Just what role the genetic material of the plant plays in this connection is not clear.

In general, it would appear that the independence of the individual structures on the grass phytomer and of the principal plant parts is more imposing than any correlations which might exist between them. Hardly any correlation can be found which can be shown to hold up under all conditions of environment. Mention has already been made of the lack of relation between leaf width and the presence of shoots. Brown (1940) found a relation between leaf width and number of rhizomes, but he sampled only two strains. The correlation of short leaves and many tillers is not dependable beyond the limits of normal domestic types. Even the correlation between culm blade length and internode length (text-fig. 27) would break down if more extreme habitat types were included. The importance of this independence of the phytomer to variation in bluegrass cannot be exaggerated. It permits a given plant or group of plants to record, in detail, the variations in its environment. It leads to an inevitable confusion in field and herbarium between induced variants and ecotypes. It likewise greatly increases the problem of recognizing and classifying strains and varieties. So-called clonal differences frequently reflect different treatment rather than different inheritance.

It is especially striking, and in the author's opinion not at all accidental, that the criteria, or combinations of criteria, which differentiate one strain or ecotype from another appear to be the very ones which are included in the repertoire of characters which can be produced by environmental manipulation or variation. The important question is why, in one case, these characters should be stable enough to be passed on to offspring, while, in the other, the same characters are theoretically only temporary. How is stability achieved?

It does not seem reasonable that this thoroughgoing similarity of induced and inherited characters should be the result of two entirely different causes. It seems more likely that morphological (and therefore physiological) response to environment and genetic change are inextricably bound together in higher plants just as they appear to be in simpler forms of life, and that drawing a line between inheritance and environment at the finer taxonomic levels is impossible.

SUMMARY

A three-year study of Kentucky bluegrass has been made with emphasis placed on the morphology and growth of the individual plant and its variation with season and environment. In addition to extensive field observations and tests, laboratory experiments and micro-dissections have been made. Previously published and unpublished work has been synthesized with these investigations in an attempt to produce as complete and readable an account of the life history of the grass plant as possible.

A grass plant is built of morphological units called phytomers. These units are produced from the growing point. They potentially consist of a leaf blade and sheath, and the internode, bud, and pair of roots immediately below this leaf. Only infrequently are all structures present and fully developed. In various combinations they unite to produce the characteristic parts of the mature plant. Ultimate simplicity is achieved in the flowering shoot where the last phytomer of the culm consists only of a much-attenuated internode.

Just as the form of the plant depends on which phytomer structures are present, so also does its growth depend on the sequence of maturation and elongation of the phytomer parts. This sequence begins with the rise of the leaf blade from the growing point, and its subsequent elongation. The leaf sheath follows, and then the internode may elongate or remain much compressed. The bud may begin to appear when the blade matures, and may develop into a shoot while the sheath is elongating or remain dormant indefinitely. Roots are usually the last structures to develop.

While the individual parts of the phytomer, and the phytomers as a whole, show considerable originality and variation, they characteristically tend to organize into three main types of shoots—the rhizome, the tiller, and the flowering shoot. These structures are analyzed with respect to their morphology and manner of growth. The basic phytomer patterns are found to hold with few exceptions.

The critical region of the bluegrass plant is the nubbin of short internodes just beneath the soil surface, to which the leaves attach and from which the three shoot types arise. This area contains the reserve supply of buds, the suppression or development of which determines what the plant will look like and what it will do.

A bluegrass plant can be interpreted on a seasonal basis, just as though it were a winter twig or a pine bough. This requires careful study of the crown area and a knowledge of progress of basic seasonal events such as flowering, tillering, and dormancy. By examining the number of phytomers, length of leaves, whether the buds develop, the position of these buds and the kind of shoots they produce, a complete picture of the year's activity can be drawn. Such a study can be used to provide an understanding of the type of plant to be expected in a given locality or habitat, under different management regimes, or in specific seasons. The structure of the crown region is of great importance in experimental tests, both laboratory and field, and statistical planning and analyses for the response obtained under

any situation will vary greatly depending on what type of plant is dominant in the experimental material.

A plan of practical management of bluegrass must first take into account to what use we intend to put it, so that we can decide what kind of a plant we need. We are then in a position to apply specific treatments to the sod. The effects of various environmental factors and treatments on grass plants have been discussed in detail with reference to their influence on specific parts of the plant.

From a taxonomic and genetic point of view it cannot be emphasized too strongly that bluegrass is flexible and that its final form is largely the result of specific environmental influences which are often brief in duration, rather remote in time, casual in distribution, and specific in effect. While under certain limited conditions correlations between various organs of the plant may exist, if populations from sufficiently diverse habitats are examined most correlations will be considerably altered and may break down completely. A study on variation in bluegrass with reference to this situation is in progress at the present time.

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EXPLANATION OF PLATE

PLATE 2

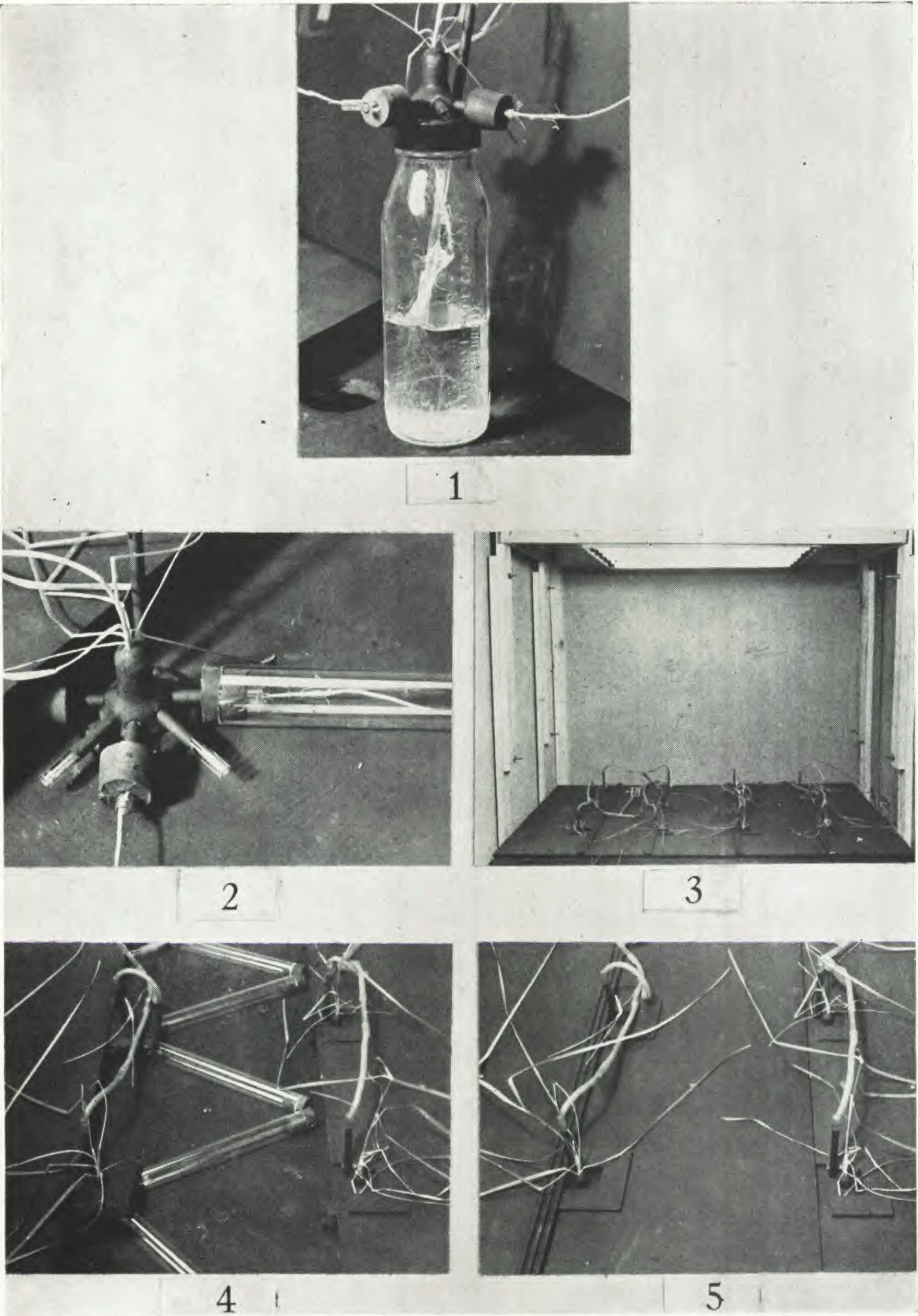
Fig. 1. Baby bottles made it possible to watch how bluegrass grows. (Some of the nutrient solution was removed to show roots and capillary tube supplying air.)

Fig. 2. Close-up of the top assembly with rhizome chamber attached and a rhizome extending into it.

Fig. 3. The bottles were placed in a light-tight box, provided with air bubbled under pressure, and the rhizome chambers concealed beneath a series of panels.

Fig. 4. One of the panels removed exposing rhizome tubes.

Fig. 5. View of the plants with panel in place.



ETTER—HOW KENTUCKY BLUEGRASS GROWS



6



7

ETTER—HOW KENTUCKY BLUEGRASS GROWS

EXPLANATION OF PLATE

PLATE 3

Fig. 6. A confusion of long green midsummer leaves trodden into disarray by cattle.

Fig. 7. Underneath the summer grass is an equally confusing tangle of wiry stems, the rhizomes. The soil has been washed away under a stream of water.

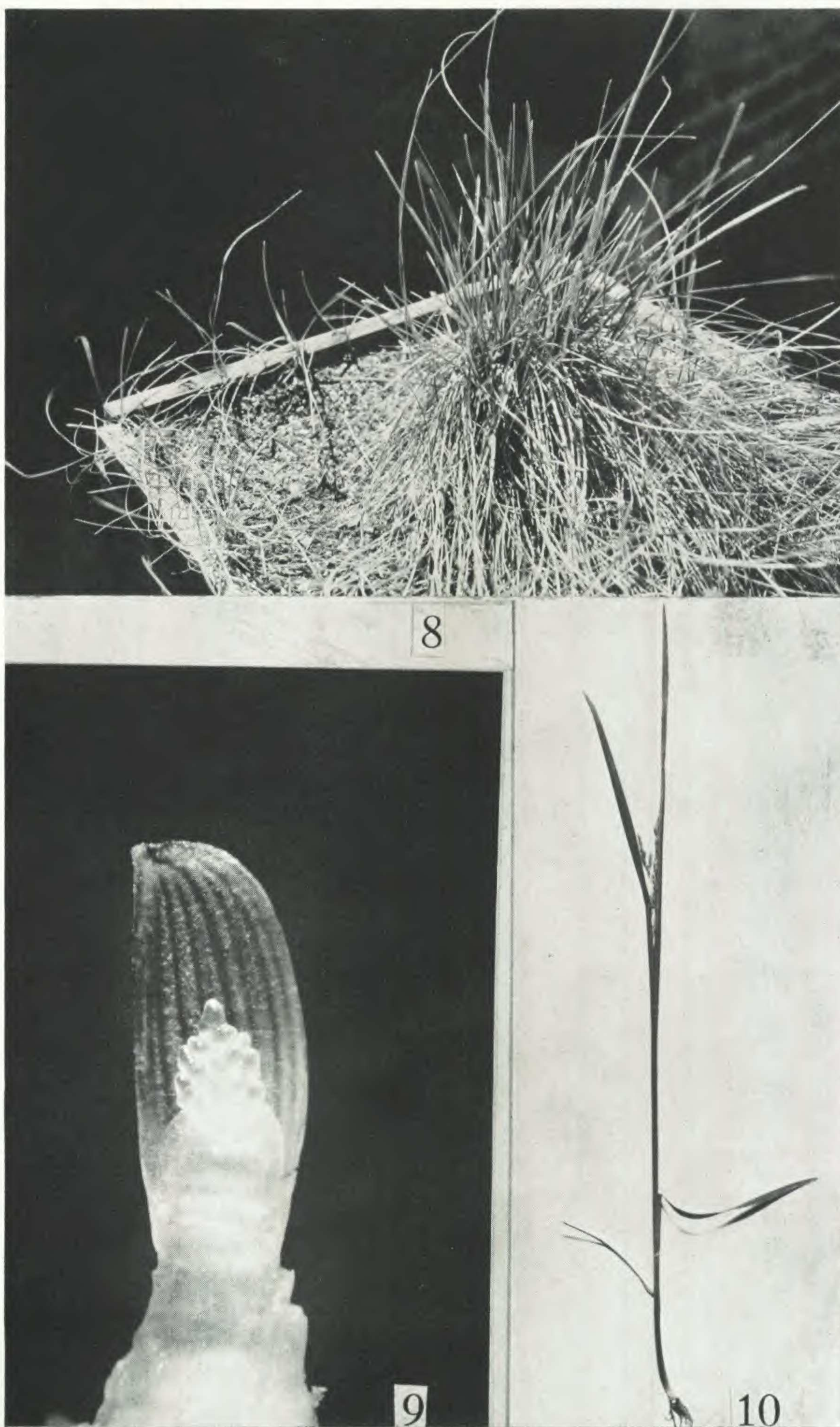
EXPLANATION OF PLATE

PLATE 4

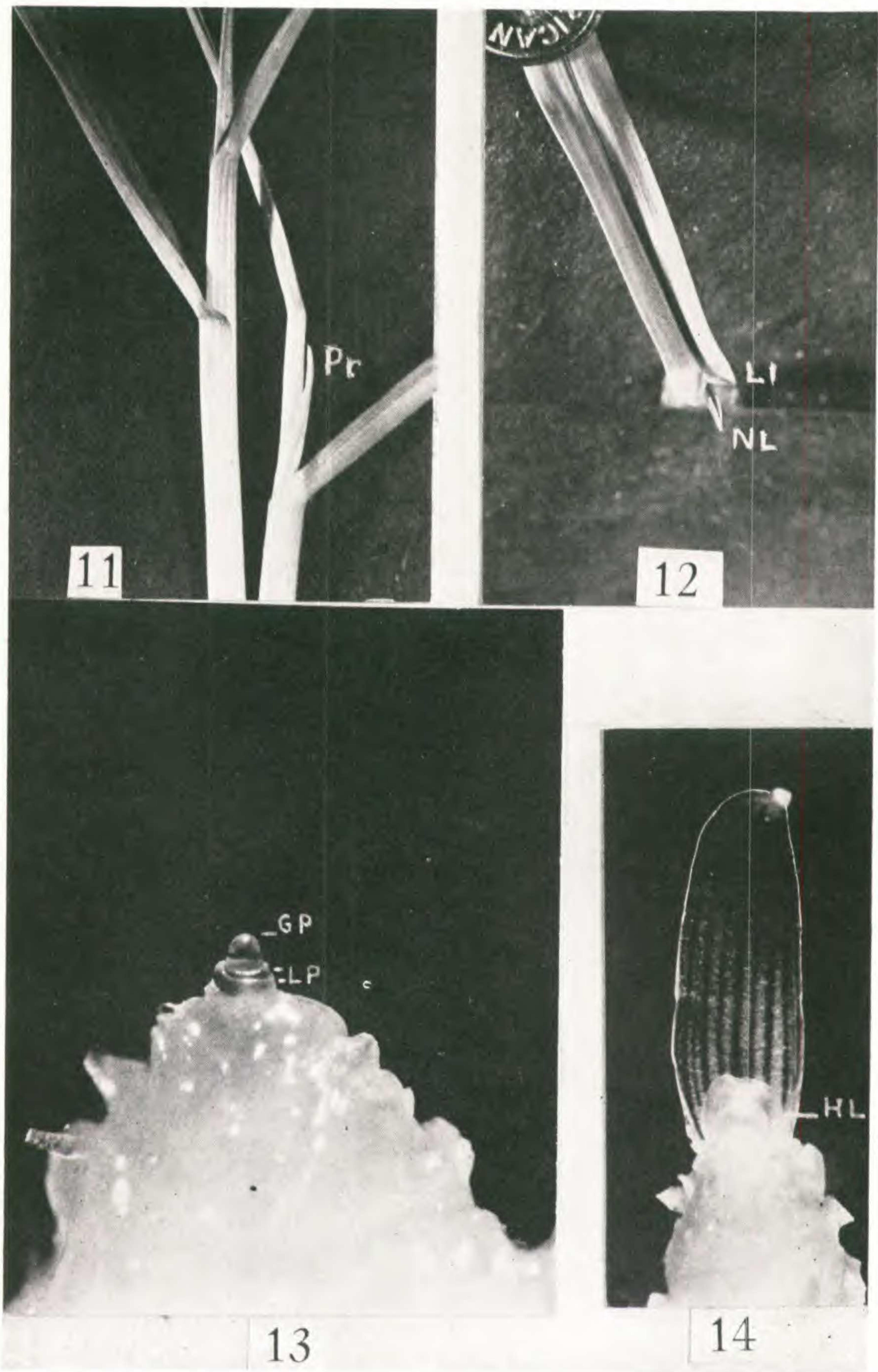
Fig. 8. A bluegrass plant and its undernourished offspring. Large parent plant has its roots in a pot of soil underneath the tray. Small plants along the left edge are turned-up rhizomes having only sterile "vermiculite" to feed on.

Fig. 9. An early stage in the development of a flowering shoot. Half of the "younger" leaf (the banded leaf in back) has been removed, showing the youngest or "hood" leaf within, and the proliferating growing point protruding through the hood. (Photo by Dr. O. T. Bonnett, of the Agronomy Department, University of Illinois.)

Fig. 10. A young flowering shoot with the panicle just appearing from its enclosing sheaths.



ETTER—HOW KENTUCKY BLUEGRASS GROWS



ETTER—HOW KENTUCKY BLUEGRASS GROWS

EXPLANATION OF PLATE

PLATE 5

Fig. 11. Successive sheaths enclose each other, but the blades bend outward at their junction with the sheath. The lowest leaf on the right clasps an intravaginal shoot with one leaf bent to the left. The prophyll marked *Pr* is still visible between them.

Fig. 12. Looking down on a bluegrass leaf. The blade is clipped with a thumb-tack, and the ligule is marked *LI* and the new blade coming up through it is *NL*.

Fig. 13. The bulbous translucent growing point of bluegrass, and two leaf primordia. (Photo by Dr. O. T. Bonnett, University of Illinois).

Fig. 14. Young leaves rising from the stem apex. Hood leaf is indicated by *HL*. (From Musgrave, 1940).